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UPSTREAM MIGRATION OF *LEPTOPHLEBIA CUPIDA* NYMPHS

(EPHEMEROPTERA: LEPTOPHLEBIDAE)

IN THE BIGORAY RIVER, ALBERTA

by



WORTH HAYDEN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1971





UNIVERSITY OF ALBERTA  
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and  
recommend to the Faculty of Graduate Studies for acceptance,  
a Thesis entitled Upstream Migration of *Leptophlebia cupida*  
Nymphs (Ephemeroptera: Leptophlebiidae) in the Bigoray  
River, Alberta, by Worth Hayden in partial fulfilment of  
the requirements for the degree of Master of Science.



## ABSTRACT

The migration of *Leptophlebia cupida* (Say) nymphs was studied in April of 1969 and 1970 during the period of ice break-up in the Bigoray River. This river is located in west central Alberta, and is a typical, slow moving, brown-water stream that drains an extensive muskeg area. The study area comprised two pools and two riffles of the river, and an extensive marshy area, draining into the uppermost pool via an intermittent tributary. During the high water level period associated with ice break-up in the spring, the nymphs of *L. cupida* moved upstream along the edges of the river and into intermittent tributaries flowing into the river. The proximal stimulus for migratory behavior was found to be the high, turbulent flow associated with the spring run-off. Neither temperature, chemical conditions, nor the population density of *L. cupida* could be correlated with the nymphal movement. The nymphs stopped migrating into the tributary areas when the water of the river dropped below a certain level. Movement within the tributary areas ceased when the nymphs reached a thawed, still-water habitat of a semi-permanent nature. The route that the nymphs would take in the marshes seemed to be associated with abrupt chemical gradients of the water.

The migrating nymphs were day active. Following migration, drift samples indicated that *L. cupida* exhibited the typical mayfly behavioral drift pattern; that is, greatest drift densities at night. The immigrant nymphs emerged from the swampy tributary areas and the female imagos oviposited back in the river.

The adaptive significance of the *L. cupida* migration is discussed. Finally, comparisons are made between the *L. cupida* migration and insect migrations in general.





## ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. H.F. Clifford for suggesting this problem, and for guidance and critical review throughout the research and during the writing of the thesis. Thanks are also due Dr. B. Hocking and Dr. A. Steiner for their suggestions and review of the manuscript.

Graham Daborn deserves special acknowledgement for his many hours of helpful discussion, assistance in the field, and finally for critically reading the thesis. Don Pezzot served well as a field and laboratory assistant during the summer of 1969. Bill Bond and Pat Lloyd offered much help in field work, and Tom Christison and Jerry Kisabeth set up the plotting program used in drawing some of the graphs. For their companionship and criticism I would like to mention K. Dietz, K. Horkan, E. Moodie, L. Noton, and R. Walsh. To these people I express my thanks.

Financial support was provided partly by teaching assistantships from the University of Alberta and partly by monies from the National Research Council through operating grants to Dr. Clifford.

I am particularly grateful to my wife Rhue for her patience, understanding and encouragement during the preparation of the thesis.





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## INTRODUCTION

Insect migrations have been known for many years, but only in the last few decades has the phenomenon received much detailed attention. Recent studies have corrected a number of misconceptions about insect migratory behavior, and now some general and unifying concepts have emerged that give researchers a much more solid and realistic base to build upon (Kennedy 1961, Southwood 1962, Carthy 1965, and Johnson 1969). According to Johnson (1969) the migratory insect flight is usually an "ontogenetic response to factors heralding adversity" rather than being stimulated by an "immediate response to current adversity." Recent interpretations of insect migratory behavior require consideration of evolutionary aspects of polymorphism, either of the whole species or of populations in certain geographical regions. Through selective pressures local populations could evolve migratory behavior as an adaptation to regularly occurring adverse habitat conditions. Ehrlich and Raven (1969) present a strong argument that gene flow is perhaps much more restricted within a species than has been previously assumed. Hence differentiation within a species could result in rapid evolution of, for example, migratory behavior. They conclude by stressing local interbreeding populations rather than species populations as the important evolutionary units.

Following this line of reasoning, I feel that migratory behavior is a feature of more northern populations rather than a species population characteristic of *Leptophlebia cupida* (Say). My study was concerned with the upstream nymphal migration of *L. cupida*. These migrations occur during the spring break-up of ice in northern rivers and lakes and were first described by Neave (1930) and subsequently by Clifford (1969).



Other workers have found *L. cupida* in locations and conditions that would indicate a migration (Traver 1925, Prater 1969). After the spring run-off, Ide (1935) found mature nymphs of *Leptophlebia nebulosa* (Walker) (*Blasturus nebulosus*) as well as *Siphonurus quebecensis* Provancher and *Arthroplea bipunctata* McDunnough in a newly formed snow-melt pool some distance from permanent water. Harker (1953) has also reported an apparent migration of *Ecdyonurus torrentis* Kimmins in a Lancashire stream of England. All of these reports are of annual migratory cycles, usually resulting in many migrating nymphs moving out of permanent water and becoming isolated in temporary pools. The nymphal movements reported by Wodsedalek (1912), Moon (1940), Bishop and Hynes (1969b), and Hultin, Svensson and Ulfstrand (1969) are different from the above in that they are not seasonally restricted and they are of a dispersive nature, or they do not result in the nymphs leaving permanent water.

The spring-time migration of *L. cupida* in the Bigoray River of west central Alberta was pointed out to me by Dr. Clifford in the autumn of 1968. In the Bigoray River, *L. cupida* is a univoltine species. Nymphs hatch and grow rapidly in summer and autumn, but much more slowly in winter. Growth and maturation resume the following spring. At ice break-up in the spring, the nymphs migrate upstream, many moving into tributaries of the river from which the subimagos later emerge.

The goals of my investigation were to study and elucidate the character of the migration, the possible environmental factors stimulating the onset of migration, and the influence of the migration on the structure of the *L. cupida* population.

Although it is known that insects must be "primed" before migratory



behavior can be stimulated (Kennedy 1961), these physiological aspects are dealt with only speculatively in my study. The possible effects of a long period of ice cover and low temperatures on nymphal migration were considered even though light and temperature effects are difficult to separate because of their co-occurrence. Bishop and Hynes (1969a) have shown that during late winter, ephemeropterans become relatively less prevalent in the drift of the Speed River, Ontario. Waters (1962, 1966) also observed a decrease in drift during the winter, and he felt this was due to low temperatures. Moon (1940) mentions the probable effect of temperature on the general movements of fresh-water invertebrate faunas, but does not discuss the effects of extended periods of low temperatures. There is some evidence that extended periods of darkness can cause a breakdown in drift patterns (Bishop 1969), and Chaston (1968) has shown that endogenous behavior is often apparent only when exogenous factors (e.g., photoperiod) are repressed. There is no question that light and temperature do influence fresh-water invertebrate behavior, but what role, if any, they play in the migration of *L. cupida* is unknown. All reports of *L. cupida* migrations are, to my knowledge, from streams and lakes that are ice covered during the winter.

Nymphal habitats and food supply are also closely related. Since *L. cupida* nymphs are usually found along lake shores and river banks, especially among emergent vegetation, the nymphs would be displaced from their summer habitats in any area where thick ice formed in the winter. This displacement, especially in rivers, possibly would put the nymphs in an unfavorable stress situation that might act as a "primer" for a subsequent migration stimulus.

The availability of food would undoubtedly change as a result of





winter relocation of the nymphs. Brown (1961) and Chapman and Demory (1963) have shown that not only does the diet of aquatic insects vary seasonally, as the result of the seasonal variation of food, but large and small nymphs of the same species also feed differently. *L. cupida* is a herbivore with an apparent preference for periphytic diatoms (Traver 1925), but qualitative examination of gut content of winter nymphs would probably reveal detritus to be the important food item at this time. A seasonal change in diet (i.e., from summer herbivore to a winter detritivore) would undoubtedly have some effect on the nymphs' physiological state, which in turn would probably influence the migration. In fact Neave (1930) found *L. cupida* nymphs that had been kept in the laboratory during the winter, and which were well fed on fresh plant material, had no migratory tendencies in the spring when migration was occurring in the field. It is likely that the physiological state of the nymphs influences the initiation of migratory behavior, and food would have a great effect on the nymphs' physiological state. This is not to say that the migration is an actual search for food; instead a limited or changed food supply during the premigration period may have a conditioning or priming effect on the nymphs that would make them susceptible to a subsequent stimulus for migration.

For presentation, this thesis is divided into three main sections: Premigration, Migration, and Postmigration. Included in the latter two sections are short discussions. Finally, a general discussion relates the migration of *L. cupida* to that of insect migrations in general.



## DESCRIPTION OF STUDY AREA

The north fork of the Bigoray River ( $53^{\circ}30-1/2'N$  by  $115^{\circ}25-1/2'W$ ) is a brown-water stream that is part of the Mackenzie River drainage. The stream has little gradient. For most of its length (approximately 80 km) it is a relatively deep, slow moving, typical muskeg stream. Riffles RA and RB of the study area and the long, straight riffle just downstream from RA (Figure 1) are the result of rechannelling and road building operations; they are atypical of most of the river. Pools PA and PB are about 2 to 3 meters deep and have soft muddy bottoms. During the summer, considerable amounts of aquatic vegetation appear in the river, especially in areas RA and PB. The general drainage character is that of muskeg and marshy areas draining into the river via intermittent tributaries.

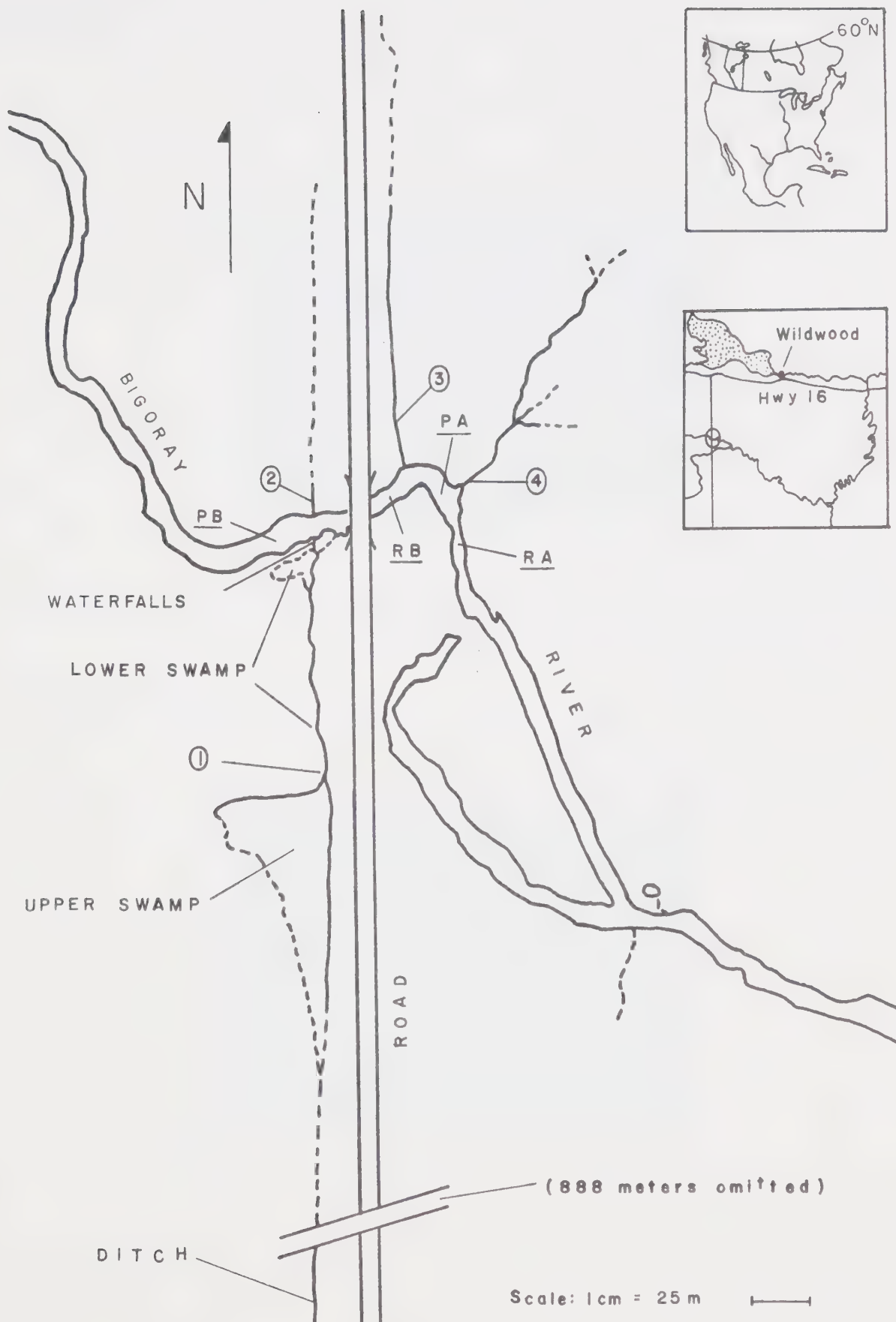
The main tributary studied was Tributary 1 (Figure 2), which drains northward into the Bigoray River; a few meters before it enters the river the tributary passes over a small waterfall about 80 cm high. The lower swamp drained by Tributary 1 is of sedge hummocks and in the northern half there is enough gradient for a detectable flow of water. About 100 meters south of the river, the upper end of the lower swamp is constricted, forming a neck through which the upper swamp drains. The upper swamp, which covers an area of approximately  $1000\text{ m}^2$  and is from 50 to 80 cm deep throughout the summer, is characterized by a *Carex - Equisetum - Drepanocladus* floral association, bordered on the west by *Sphagnum* and on the east by a road. To the south of the upper swamp, lying parallel to the road, is a shallow marshy area cleared of trees. Approximately 400 meters south of the river a roadside ditch drains into this marshy area. The ditch originates on the hydrographic divide (1200 meters south of the river) separating the north and south forks of the Bigoray River. This







Figure 1. *Map of study area.* Dashed lines indicate intermittent flow or the boundaries of migration. 1, Tributary 1; 2, Tributary 2; 3, Tributary 3; 4 Tributary 4. RA, lower riffle; PA, lower pool; RB, upper riffle; PB, upper pool.







- Figure 2.
- a. *Looking north across lower swamp toward the Bigoray River.*
  - b. *Looking south across upper swamp toward the hydro-graphic divide.*







ditch is steep enough to cause a number of rapid water areas, but the top of the divide levels out into mossy pools that are 30 to 50 cm deep.

During summer, much of the Bigoray River drainage is of a temporary nature, but it is probable that the upper swamp always retains water throughout the ice-free period.

Tributary 2 also flowed over a waterfall before entering the river, but flowed only during break-up and its drainage area was much less extensive. A definite water channel was confined to the last few meters of this tributary—otherwise this area was much like the zone between the upper swamp and the ditch of Tributary 1. Tributary 3 was little more than a drainage ditch between the road and a *Sphagnum* bog to the east; however, in its upper end, Tributary 3 drained a small sedge and moss filled area. Water, probably originating from the *Sphagnum* bog, flowed in this region during the entire summer of 1969. Tributary 4 flowed through and drained a large part of the *Sphagnum* bog mentioned above. Discharge from Tributary 4 was greater than from either Tributary 2 or 3, and equal to or perhaps slightly greater than that of Tributary 1.



## METHODS

Physical, chemical and biological sampling was conducted throughout the 19 month study period at approximately monthly intervals. In the spring of 1969 and 1970, during the migration, a field trailer was moved to the study area, allowing observations to be made and samples to be taken more frequently.

### Physical Methods

River temperatures in the center of the lower pool (PA) were continuously recorded from 8 October 1968 to 12 October 1969 and again from 12 April 1970 to 1 June 1970 using a Ryan model D-30 thermograph. At other times temperatures of the river were taken with a hand thermometer. For the 12 April to 1 June 1970 period, a second Ryan thermograph was placed in Tributary 1, at the constriction between the upper and lower swamps.

The relative water level of the river was measured from a meter stick attached to one of the bridge pilings in the vicinity of the upper riffle (RB). These readings were incomplete during the winters because in both years the river water froze into the substrate at this site.

River discharge was measured in the lower riffle (RA) on several occasions using a Gurley direct reading current meter (model #665). Measurements were repeated at  $1/4$ ,  $1/2$ , and  $3/4$  the width of the stream, with the instrument held at mid-depth at each point and the average of these readings taken as the velocity. Channel depth was calculated by summing the depths at  $1/4$ ,  $1/2$ , and  $3/4$  the width and dividing this number by 4, thus compensating for the channel margins. Discharge from the tributary was measured by placing a 10 liter plastic bucket under the waterfalls and recording the filling time of the bucket. This method was





accurate only during periods of low discharge.

Measurements of light attenuation in the river water and through the ice/snow cover were taken using a Gemware submarine photometer (model #268-WA-310) equipped with Weston selenium photocells covered with cosine filters. Spectral composition of the underwater light was determined by placing red (#29), blue (#47), and green (#13) filters over the sea cell. Field procedure was for one person to face the sun with the sea cell in front; the cell was then lowered into the water at 10 cm increments, first without the colored filters and then with each colored filter over the covering cosine filter of the sea cell. A second person recorded the milliamp and microamp readings of the deck cell and the sea cell. Sub-ice readings were obtained by lowering the sea cell into the water through a hole in the ice and then covering the hole with a piece of plywood. All readings were taken in the lower pool (PA) of the river. The values were graphed on a semilog scale. The lines obtained for all light readings describe the character of attenuation based upon the percentage of surface light at various depths. Methods outlined by Westlake (1965 & 1966) were used to interpret the data.

Color and turbidity were measured photometrically using a Hach model DR-EL portable laboratory kit. The color measured was apparent color since no attempt was made to separate suspended material from the water sample. Conductivity was measured with a Beckman model RB3-338 portable conductivity meter.

#### Chemical Methods

River water samples were taken at intervals of approximately one month from either river area RA or PA, both being downstream from the mouth of



Tributary 1. Samples were collected from mid-depth with a 2 liter Kemmerer bottle. Determinations of pH, alkalinity, total and calcium hardness, orthophosphate, and total iron were made using the Hach kit. All determinations were done in the field except for the 8 November 1968 water sample. For this sample a drop of chloroform was added to the water sample and analyzed later in the laboratory. The Alsterberg (Azide) modification of the Winkler method was used to measure dissolved oxygen, and Rawson's nomogram used to convert parts per million (p.p.m.) to per cent saturation. Tributary 1 water was analyzed in the same manner as mentioned above. This water was collected in the vicinity of the waterfalls until low water level made this impossible; thereafter samples were taken from the north end of the upper swamp.

During the spring (or migratory) periods of 1969 and 1970, more frequent chemical analysis of the waters was done in the field, and on two occasions (16-17 April and 8-9 May 1969) water analysis was carried out at 3 hour intervals over a 24 hour period.

#### General Biological Methods

For the migratory study quantitative samples were desired for estimates of population densities and numbers. The difficulties of "quantitative" sampling are well known (Cummins 1962), and in my study these problems were amplified by the wish to compare samples from three different types of aquatic habitats: riffles, pools, and heavily vegetated swamp areas. A sampler was needed that would function properly in all three situations and yield comparable results. However, none of the standard samplers were suitable for all three of these situations.

To overcome this problem, a hand operated, 10 cm diaphragm pump with



an overpour discharge was used (Figure 3). The pump was mounted on a metal sled so that it could be pulled to the sampling sites in both winter and summer. A mesh bag (1 mm mesh opening size) was fitted around the pump discharge to retain the material once it was pumped through, and a 5 m section of rubber hose was attached to the suction end of the pump. The area to be sampled was delimited by quickly lowering an appropriate length of stove pipe, 20 cm in diameter, to the stream bottom and then forcing the pipe further into the substrate. Holes had been drilled in the lower 40 cm of the pipe and fine mesh (0.5 mm mesh opening size) brass screening soldered over the holes. This allowed water surrounding the pipe to flush the area being sampled, and the water also stirred up the substrate.

Pump samples were taken from 1 February 1969 to 3 May 1970. During the winter, holes for the 20 cm pipe were cut in the ice with either a chain saw equipped with an ice chain or a 30 cm power ice auger. The samples were either picked over in the field or returned immediately to the lab for picking. The animals were preserved in 70% ethanol.

The pump sampler had several advantages over standard stream samplers: (i) it sampled both the stream bottom and the water column over it; (ii) the placement of the pipe created very little wavefront; (iii) the sucking action of the pump and the flushing action of the water pouring through the holes in the pipe allowed collection of burrowing forms; (iv) it could be used in all habitat areas; (v) it worked equally well in winter and summer. The disadvantages were: (i) the weight and bulk of the pump and sled; (ii) the centers of deep pools could not be reached and sampled when there was no ice covering the river; (iii) the pump would not maintain its prime in water less than about 20 cm deep.







- Figure 3.
- a. *Pump sampler at the lower riffle (RA) in August 1969.*
  - b. *Pump sampler on the upper pool (PB) in February 1970.*





During the last week of May 1969, a series of riffle samples were taken to compare the efficiency of the pump with that of the Surber sampler, and a series of pool samples were taken to compare the pump with the Ekman dredge. Analysis and discussion of these comparisons are presented in Appendix A. Results from all three methods showed very high standard errors of the mean, which indicated that these data were a poor measure of actual densities of the aquatic fauna. A comparison between the sampling methods showed the pump to be a more efficient sampler than the Ekman dredge. Little difference was found between the pump and the Surber sampler.

During and after the migrations of 1969 and 1970, nymphal locations and migratory boundaries were established by collecting nymphs in the tributary areas with dip nets (0.25 mm mesh opening size). Numbers of nymphs migrating per unit time were determined by actual counts of nymphs moving upstream and downstream across a line per minute. Usually ten counts, each of 1 minute, were made during each observation. The rate of movement of the migrating nymphs was estimated by timing nymphs of various sizes over distances of 1/2 meter; these distances encompassed various current and substrate conditions. Emergence of *L. cupida* from the tributary area and river was monitored with wood framed, three-sided emergence traps, covered with green plastic screening. The effective trapping area of each trap was 0.14 m<sup>2</sup>. During the first few days of emergence in May 1969, additional subimagos were collected with an aerial insect net.

#### Drift Methods

Drift samples were taken from the lower riffle (RA) for two 24 hour periods, during (15-16 April 1970) and after migration (1-2 May 1970).





Drift nets were emptied every 2 hours. Two 0.093 m<sup>2</sup> (1 ft<sup>2</sup>) nets (0.8 mm mesh opening size) were stacked 0.8 meters from the west bank, and one net was set 1 meter from the east bank. Macroinvertebrates were picked from the samples during the 2 hour interval before the next collection, and preserved in 70% ethanol.

Nymphs and subimagos were separated into males and females and measured to the nearest 0.1 mm with a vernier caliper under a dissecting microscope. Total length was measured from the anterior surface of the head, in an hyprognathous position, to the posterior margin of the last abdominal tergite. The sexes of nymphs larger than 3.0 mm were separated by noting the development of the eyes.

#### Gut Content Analysis

Daily feeding activity of the nymphs was studied during the migration by examining the gut contents of individual nymphs taken from drift samples. The method used was a modification of the counting method discussed by Brown (1961), with quantitative values of gut content derived from counts of diatoms seen in 4 strips of a Sedgewick-Rafter cell under 100X magnification. Estimates of total numbers of diatoms were calculated by standard plankton counting procedures (Welch 1948). Preparation of the samples entailed taking the part of the gut anterior to the second abdominal segment (all the foregut and part of the mid-gut), then separating and randomly spreading the gut contents in the counting cell containing 70% ethanol. After the cover slip was in place, the contents were again uniformly spread and the cell positioned on the stage of the compound microscope for 3 or 4 minutes before counting was done.

Total length and sex was noted for each nymph used in the food study.



The relative abundance of diatoms found in nymphs from different drift periods and in different size classes was calculated by dividing the estimated total number of diatoms per dissection by the cube of the nymph's total length, and averaging these values for each time period or size class.

Several categories of food other than diatoms were initially recorded: (i) the absence or presence (scarce, some, or much) of filamentous algae; (ii) absence or presence of moss or higher vascular plant cells; (iii) relative abundance of all food material rated on a scale from 1 to 5 for each counting strip; and finally, (iv) a subjective estimate (little or much) of the amount of sand in the dissected gut. The fullness of the gut was also noted when it was first taken from the nymph. It was found that these subjective categories, other than diatom counts, were unreliable for the type of feeding analysis sought. *L. cupida* has been shown to be an efficient feeder on periphytic diatoms (Traver 1925), and previous descriptions of their gut content includes diatoms (Traver 1925, Neave 1930). The main food item found in all nymphs of the drift samples was diatoms; thus it seems justifiable to use diatoms as an indicator of daily feeding activity. Nymphs with empty guts were excluded from the analysis, since this may have indicated an impending molt.

The nymphs used for analysis of daily feeding patterns were selected at random from each sufficiently large drift sample, and later the data of each time period were proportioned by selecting equal numbers from each size class for each time period analyzed. Feeding activity with respect to size classes was analyzed by taking equal numbers of equal sized nymphs from each of the samples of different time periods. These procedures should eliminate most of the bias that size classes would have on time



period feeding analysis, and the bias that time periods would have on size class feeding analysis.



## LONG TERM PHYSICAL AND CHEMICAL FEATURES

In order to detect possible environmental stresses on *L. cupida* nymphs, especially during the premigration period, selected physical and chemical factors were monitored throughout the entire study period. These data might also prove useful in comparing this *L. cupida* migration locality with migrations in other geographical areas that may be investigated later.

### The River

#### Physical Features

Freeze-up in the study area began in mid-October of both 1968 and 1969, with the swamp freezing first, then the pools of the river, and, by the end of November, the river riffle areas. Figure 4 shows water temperatures of the Bigoray from 8 October 1968 through 31 May 1970. Ice covered the stream for nearly 5 months of the year, and temperatures were near 0 C for almost 6 months of the year.

Water level in the river increased greatly with spring run-off, starting during the first week in April of both years (Figure 4). During early spring, the response of water level to precipitation was rapid; but later in the summer, the muskeg areas served as a water reservoir that gradually released water to the river. The peak in early August 1969 was the result of a prolonged period of heavy rainfall, and the water level may have been higher than indicated, but the meter stick washed away at this time.

River discharge ranged from more than 3.0 m<sup>3</sup>/sec (106 cfs) in early August 1969, to less than 0.05 m<sup>3</sup>/sec (2 cfs) during the winter of 1968-69.

Apparent color and turbidity showed a gradual decrease during the

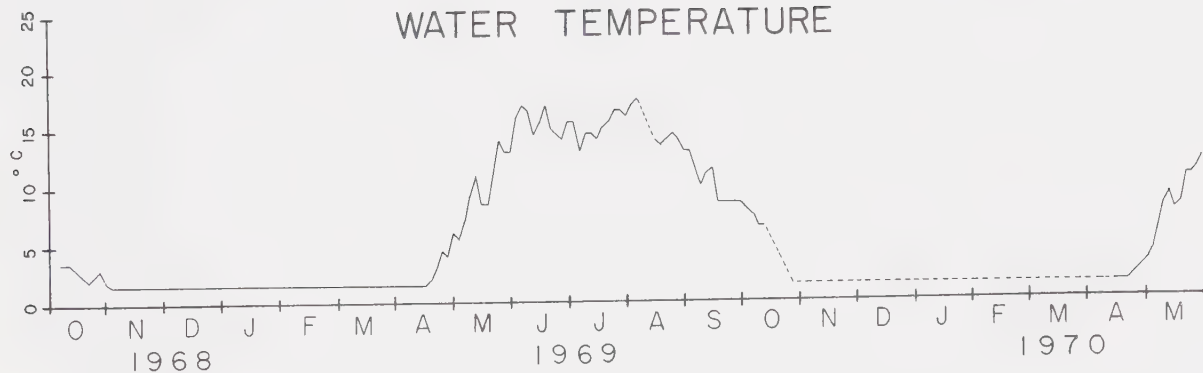




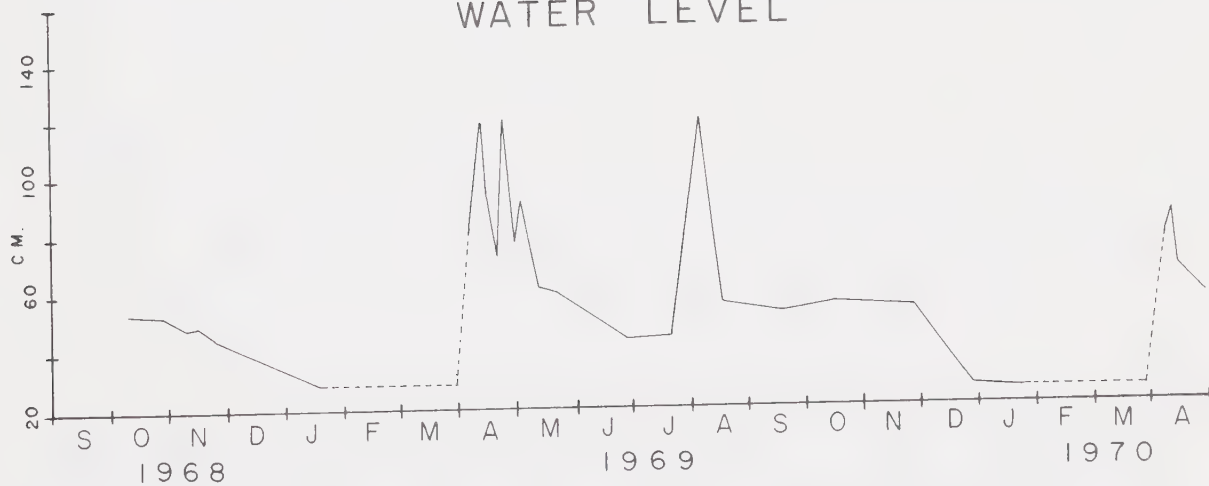


Figure 4.      *Water temperatures and water levels of the Bigoray  
River during the period October 1968 to May 1970.*

# WATER TEMPERATURE



# WATER LEVEL





autumn and winter (Figure 5), but both increased rapidly at the time of the spring break-up. Turbidity values were much higher during the early break-up of ice in 1969 than in 1970. This was due mainly to the higher water level during this period of 1969.

On 27 December 1969, an ice block was taken from PA and brought into the lab for chemical analysis. This block was cut into four horizontal sections, and turbidity, color, specific conductance, and several chemical tests were run on the melt water of each layer (Table 1). Conductivity, turbidity, and apparent color were greater in the top 18 cm than in the lower 26 cm of the ice. Part of the explanation of this is that the older top ice was formed when the river water itself exhibited a greater concentration of these constituents, but flooding over the ice in late autumn also colored the top ice. This layer of colored ice was one of the factors that diminished the penetration of ambient light through the ice, and it is probable that it is a common feature of ice formation on the Bigoray River.

#### Chemical Features

Total and calcium hardness showed a seasonal pattern inversely related to water level (Figure 6). Alkalinity was entirely bicarbonate, and paralleled the seasonal pattern of hardness (Figure 7).

Neither orthophosphate nor total iron displayed the seasonal pattern that was noted for alkalinity and hardness and which was influenced by dilution. Dissolved oxygen never reached critically low levels in the river (Figure 6). Although there was a marked decline in oxygen following ice formation in both years, there was, before the spring thaw, a late winter increase of dissolved oxygen in both years.

The river water was always either alkaline or neutral; pH fluctuations







Figure 5.      *Specific conductance, turbidity and apparent color  
of Bigoray River water during the period October  
1968 to May 1970.*

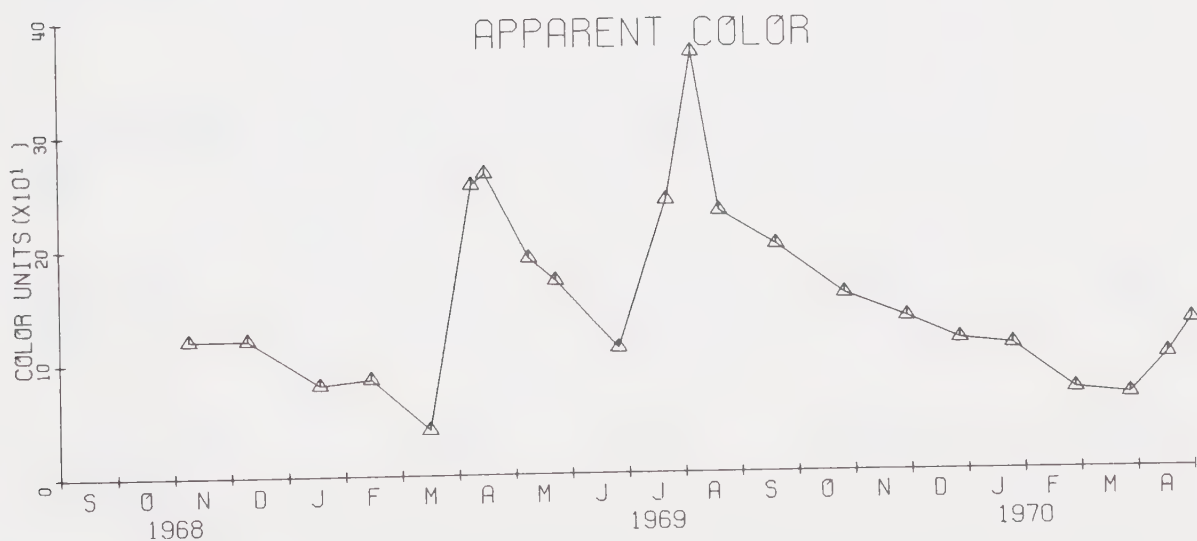
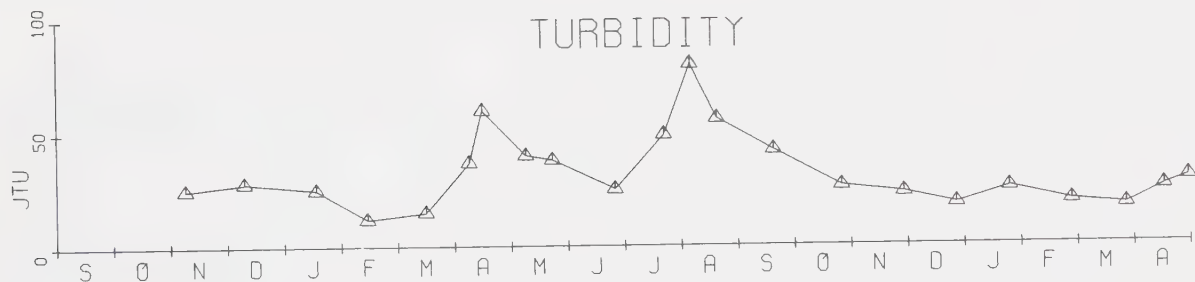
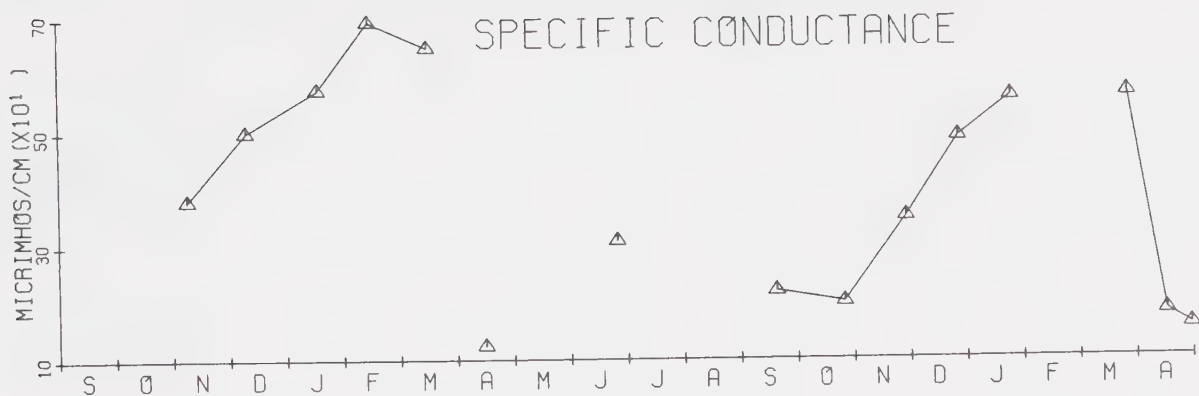




Table 1. *Variation in physical and chemical characteristics of ice from the Bigoray River, 27 December 1969.*

Depth of ice strata	0 - 8 cm	8 - 18 cm	18 - 32 cm	32 - 44 cm
Conductivity (micro-mhos)	100	170	50	50
Turbidity (JTU)	6	10	5	2
Apparent color (color units)	15	30	0	0
Calcium hardness (ppm)	20	31	3	3
Total hardness (ppm)	38	59	8	4
Orthophosphate (ppm)	0.15	0.10	0.05	0.10
Total iron (ppm)	0.13	0.12	0.02	0.02
Hydrogen ion	7.8	8.2	6.7	6.7







Figure 6. *Dissolved oxygen, hydrogen ion and hardness of Bigoray River water during the period October 1968 to May 1970.*

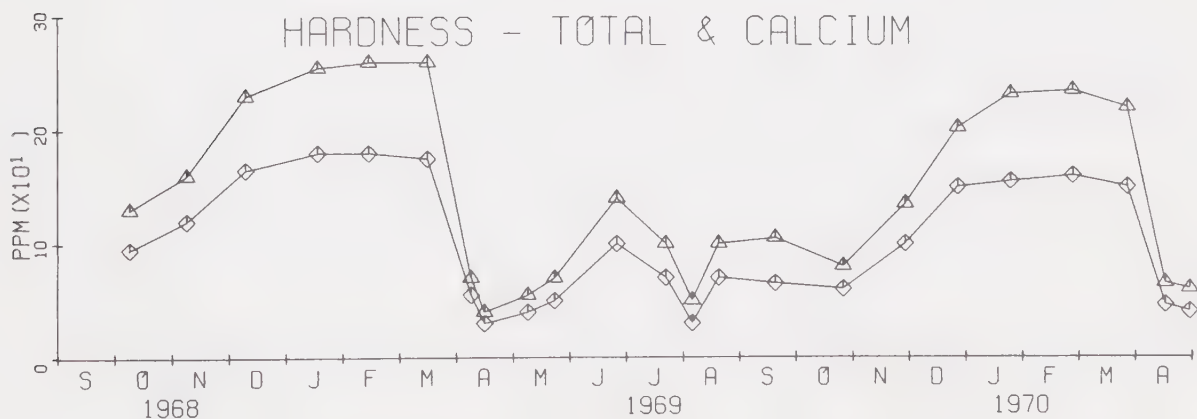
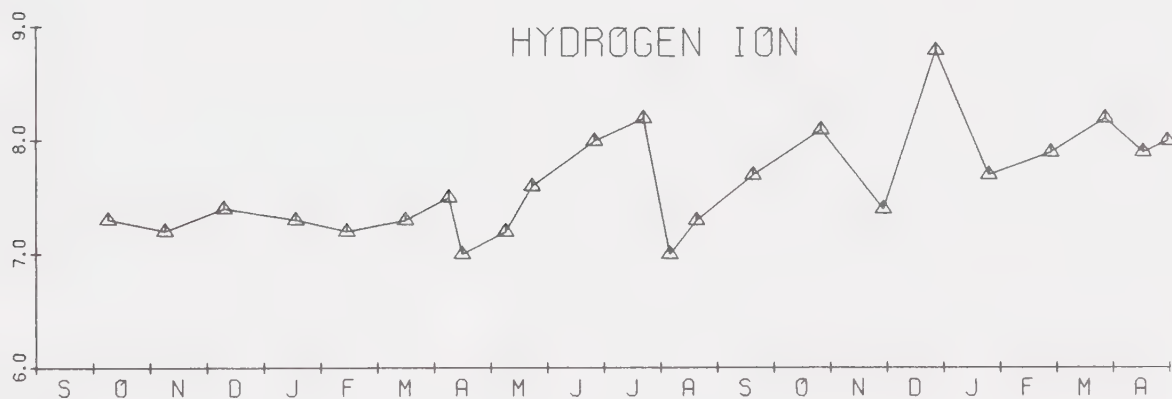
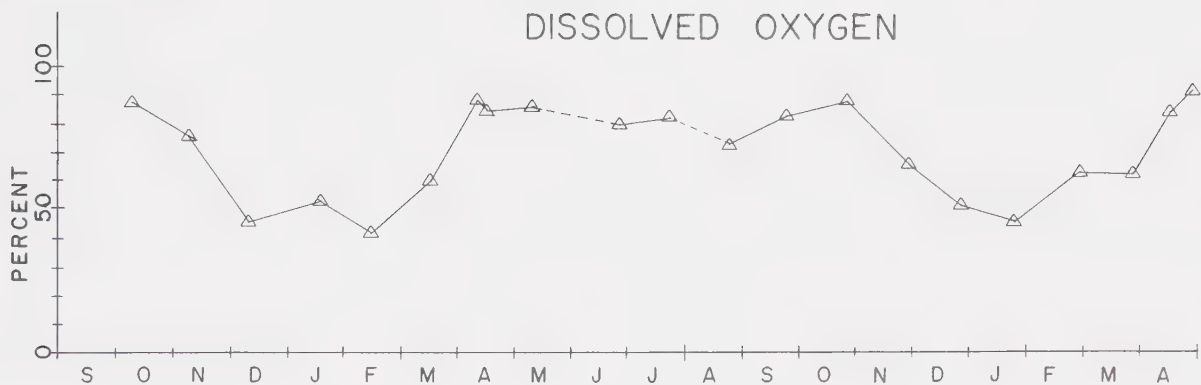
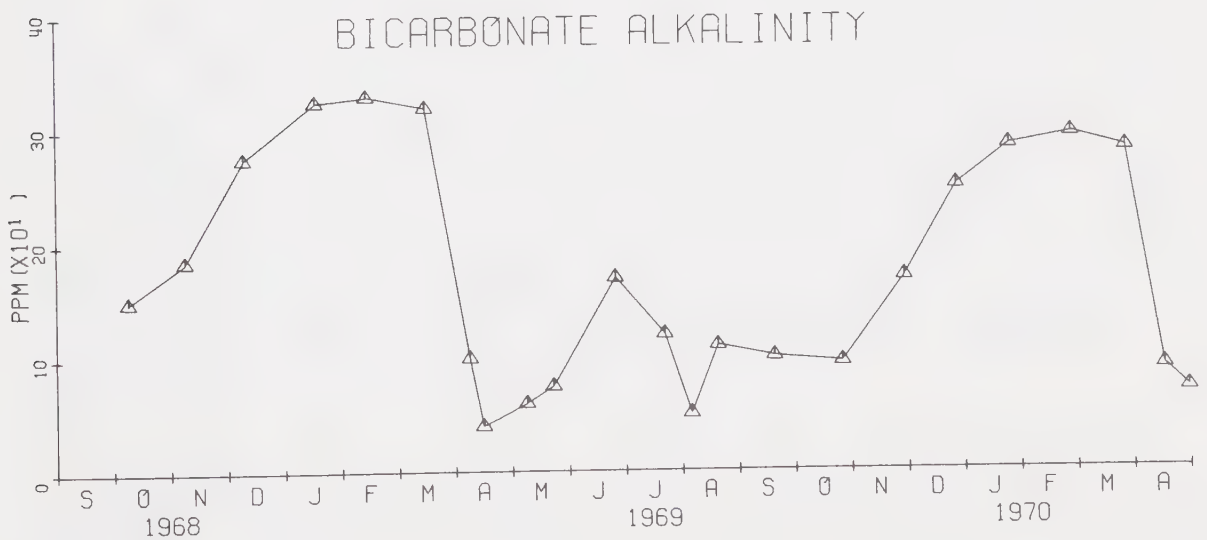
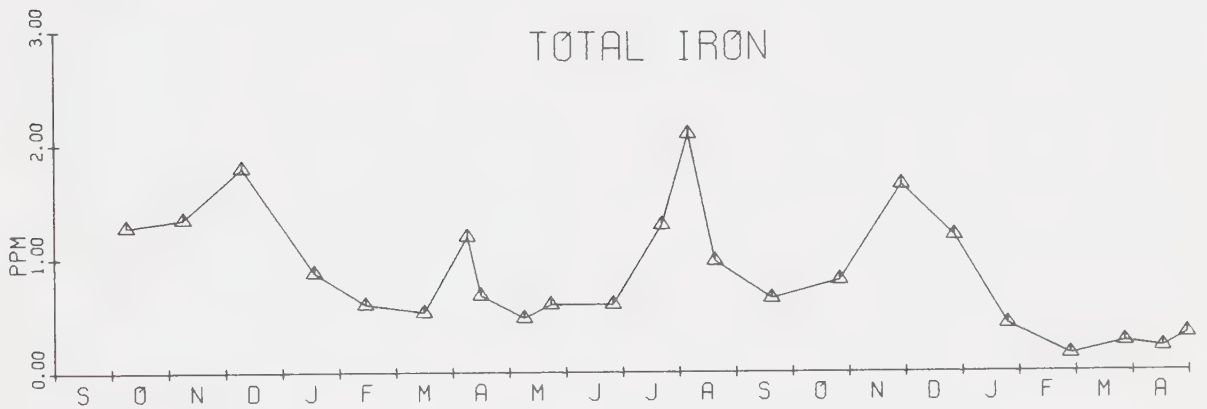
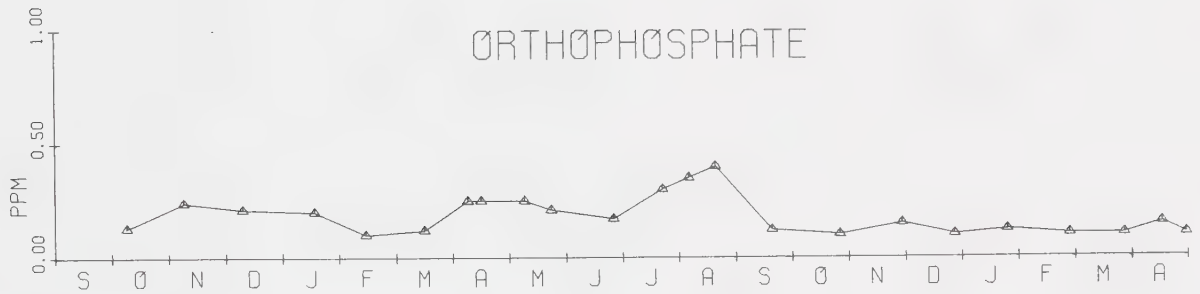






Figure 7. *Orthophosphate, total iron and bicarbonate alkalinity of Bigoray River water during the period October 1968 to May 1970.*







were relatively small, indicating a well buffered system.

## Light

The purpose of my light readings was to check for any correlation between underwater light in the Bigoray River and the migration of *L. cupida* nymphs. This aspect will be discussed in the Migration section, but the general results are presented here.

With the instrument used, absolute light values cannot be obtained, and no effort was made to convert these readings to units such as lux or foot-candles. These units are a measure of white light, and underwater light (especially in colored water) is of a different range of wavelengths (Strickland 1958, Westlake 1965). The light spectrum also changes with increasing depth in water, changing the character of total light.

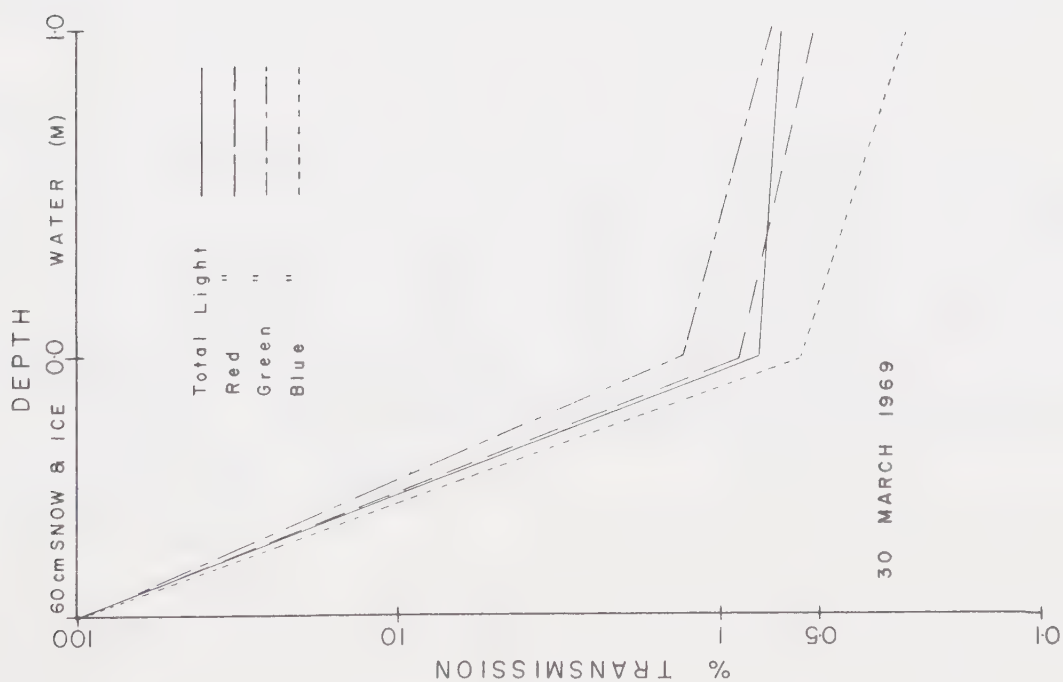
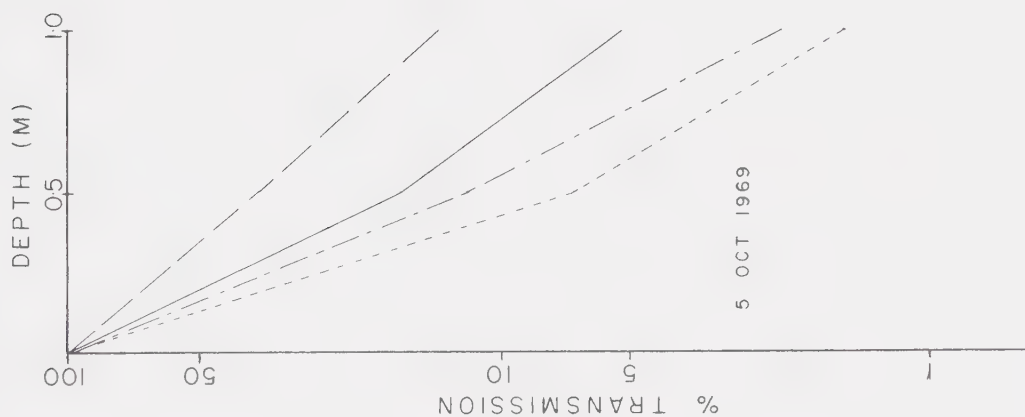
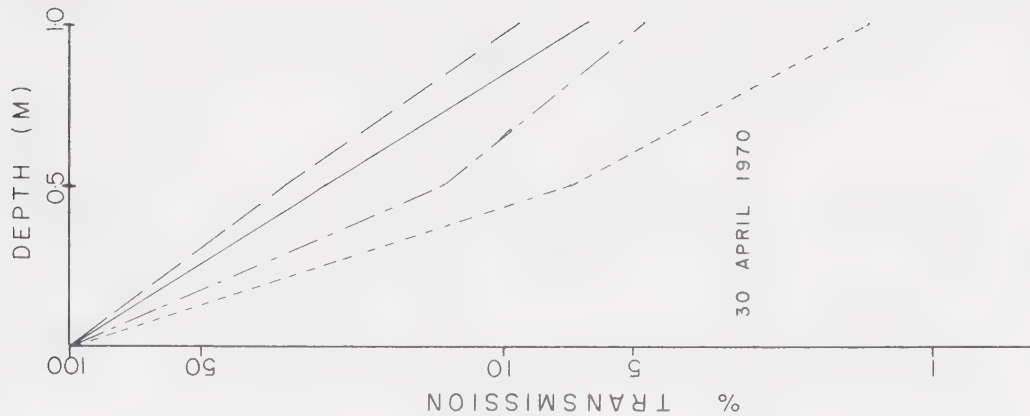
Figure 8 shows the character of light attenuation in the Bigoray River at three different times of the year. During the ice-free periods (5 October 1969 and 30 April 1970) the water was highly colored, and the rates of attenuation of the shorter wave lengths were greater than of longer wave lengths. Both ice-free dates had underwater light that showed the same spectral order of attenuation: blue greater than green, green greater than red. This spectral pattern is a result of dissolved and suspended matter (Hutchinson 1957), and it would be expected that highly colored brown water would transmit relatively more of the red light. For both ice-free readings, only 4 to 6% of the total surface light was transmitted to 1 meter.

The under-ice light readings (30 March 1969) demonstrate the great attenuating influence of ice and snow. Less than 1% of filtered or non-filtered surface light reached 1 meter of depth in the water, and only green light exceeded 1% directly under the ice.





Figure 8. *Character of transmission of red, green, blue, and total light in the water of the Bigoray River at three dates. Each line describes the light as a percentage of surface light.*





## The Tributary

### Physical Features

Tributary 1 and the upper swamp were frozen over by the end of October in both years, but water continued to flow into the river under the ice until mid-November. It was not until February 1970 that the water of the upper swamp was frozen into the substrate (it was not checked during the winter of 1969). The tributaries each had specific temperature patterns. Tributary 4 drained a *Sphagnum* bog and its water temperature rose more slowly than the temperature of the river; Tributary 1 drained a more open sedge swamp and its water temperature in the spring increased more rapidly than that of the river.

Water level in the tributaries was of course highest during the spring run-off, but discharge could not be measured during this time. Later when the level of Tributary 1 was about 1/3 of its peak level, discharge was estimated at 7.2 m<sup>3</sup>/hour (0.07 cfs). This tributary, which was the main study tributary, flowed continuously throughout the summer of 1969, but in other summers (1967, 1968, and 1970) it went dry in July or August.

### Chemical Features

Water of Tributary 1 was at times slightly acidic (Figure 9), and here the periods of lowest dissolved oxygen values also had the highest total iron concentrations (Figures 9 & 10). The tributary water had less bicarbonate alkalinity and hardness than the river (Figure 10), but as was true of the river, these constituents gradually increased throughout the summer as water level dropped.







Figure 9.      *Turbidity, apparent color, hydrogen ion, and dissolved oxygen of Tributary I water during the period April 1969 to May 1970.*

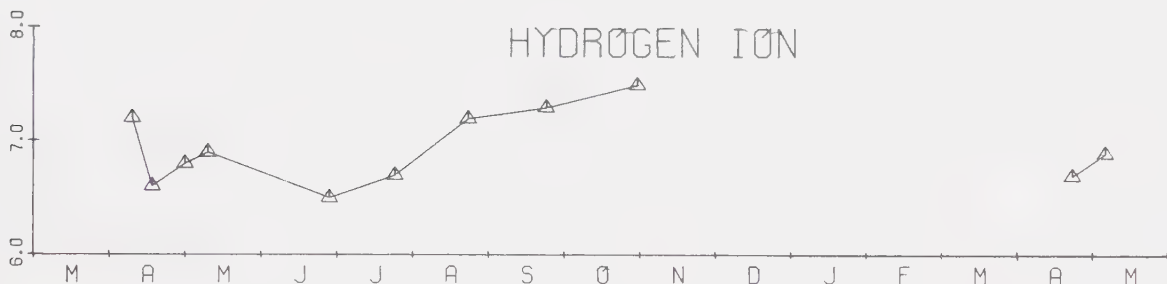
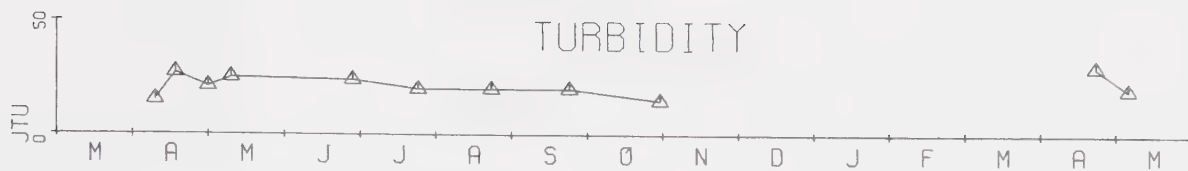
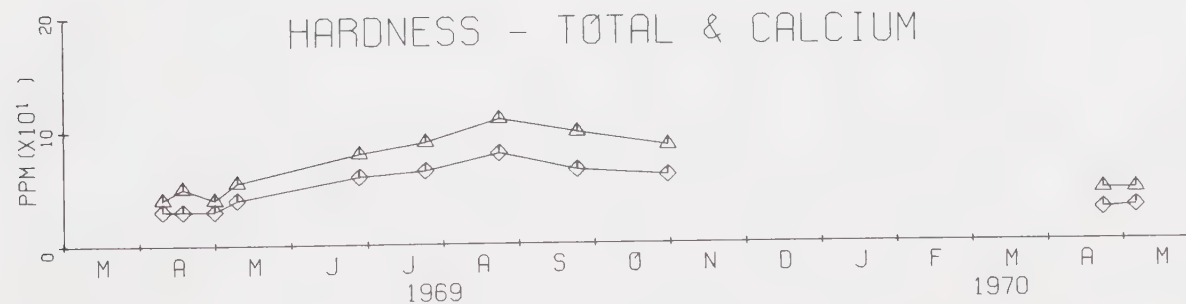
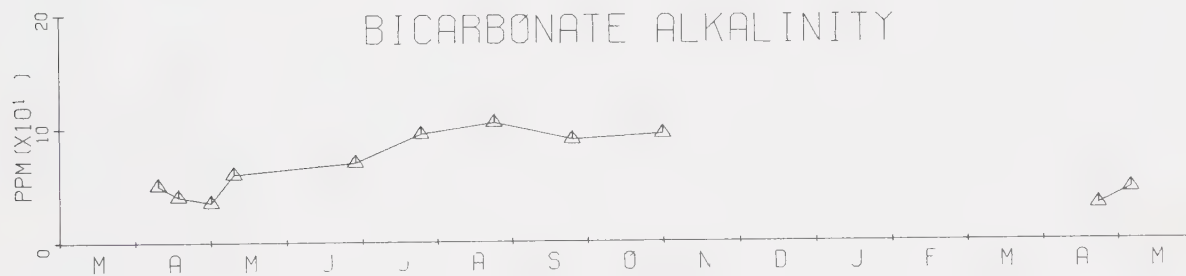






Figure 10.      *Orthophosphate, total iron, bicarbonate alkalinity,  
and hardness of Tributary I water during the period  
April 1969 to May 1970.*







## Twenty Four Hour Chemical Series

On 16-17 April 1969 and again on 8-9 May 1969, physical and chemical tests were made at 3 hour intervals for both the river and Tributary 1. This was done to monitor daily fluctuations of possible influencing factors during and after the migration of *L. cupida*. It was felt that the results of these series might elucidate factors influencing the diel behavior pattern of the migrating nymphs. The results are shown in Tables 2 through 5 and will be discussed here only in regard to daily fluctuations and their possible effects on the migration of *L. cupida*.

### 16-17 April

The water level of the river during this series showed a peak of 101 cm at midnight, and then a gradual and steady decline to 94 cm at 1500 hours on the 17 April (Table 2). Water temperature, as indicated by a pocket thermometer, ranged between 0.5 C at 1600 hours to 2.0 C from 1500 to 1800 hours. The patterns of apparent color and turbidity were similar and were affected mainly by water level. The increase of these two physical constituents during the 1800 to 2100 hour period may have been caused by muskrat activity further upstream, since several had been seen at about this time of day.

There was no 24 hour pattern for total and calcium hardness and bicarbonate alkalinity in the river. Dissolved oxygen was measured only until 0600 hours on the 17 April. The decline of per cent saturation was caused by lower temperatures, but the absolute amount of dissolved oxygen remained almost constant throughout the period. Although orthophosphate, total iron and pH each varied considerably over the 24 hour period, none apparently had a distinguishable daily pattern.

In the tributary the water level was not measured, although it



Table 2. *Physical and chemical constituents of the Bigoray River over a 24 hour period I6-I7 April I969*

Time of day	1500	1800	2100	2400	0300	0600	0900	1200	1500
Dissolved oxygen (%)	85	85	84	84	82	81			
Hydrogen ion	7.0	7.1	7.4	7.4	7.2	6.9	7.1	7.0	6.8
Total hardness (ppm)	40	45	40	45	40	40	40	40	40
Calcium hardness (ppm)	25	25	30	25	30	30	30	30	25
Total iron (ppm)	0.80	0.73	0.81	0.78	0.74	0.67	0.68	0.68	0.65
Alkalinity (ppm)	40	40	40	35	45	40	40	40	45
Ortho-phosphate (ppm)	0.30	0.15	0.10	0.15	0.15	0.30	0.15	0.30	0.20
Turbidity (JTU)	55	70	67	65	55	50	65	60	58
Apparent color (color units)	240	300	260	280	250	230	260	265	255
Temperature (C)	2.0	2.0	1.5	1.0	1.0	0.5	1.0	1.0	2.0
Water level (cm)			100	101	99	96		95	



generally showed a pattern of being highest at around 1800 hours and lowest near 0600 hours. Water temperature here increased rapidly during the day, to a high at 1800 hours and then gradually declined to a low of 1.0 C at 0600 hours.

Hardness values in Tributary 1 (Table 3) were in the same range as those of the river, and fluctuated very little. Bicarbonate alkalinity, although exhibiting a gradual decline for part of the 24 hour period, showed no daily pattern. As was true for the river, variation of dissolved oxygen in the tributary was mainly due to temperature; but the actual concentration of oxygen, which ranged between 6.5 ppm and 7.2 ppm, did increase slightly throughout the night. Orthophosphate and pH showed no cyclic patterns over the 24 hour period.

In short, for the 16-17 April series, temperature and light were the only factors that had a regular daily pattern; hence it is possible that either or both could influence the daily activity pattern of *L. cupida* nymphs during or shortly before the migratory period. The lack of a daily pattern for the other constituents would seem to discount their influence on the diel cycle of nymphal behavior.

#### 8-9 May

This series was started at 1800 hours on 8 May, and again analysis was carried out at 3 hour intervals, except for dissolved oxygen, which was measured every 6 hours. By 8 May the migration of *L. cupida* had ceased entirely; the water level had dropped in both the river and Tributary 1, and water temperatures were higher than during the earlier series.

There was no daily cycle of water level in either the river or Tributary 1 (Tables 4 & 5); instead water level declined steadily throughout the 24 hour period. Water temperatures in both areas showed the same patterns









Table 4. *Physical and chemical constituents of the Bigoray River over a 24 hour period 8-9 May 1969*

Time of day	1800	2100	2400	0300	0600	0900	1200	1500	1800
Dissolved oxygen (%)	92		86		84		86		88
Hydrogen ion	7.0	7.0	7.2	7.2	7.2	7.2	7.2	7.2	7.2
Total hardness (ppm)	60	50	52	52	56	60	55	60	55
Calcium hardness (ppm)	40	32	40	32	42	40	40	40	40
Total iron (ppm)	0.45	0.45	0.47	0.50	0.50	0.45	0.48	0.49	0.45
Alkalinity (ppm)	50	50	50	52	53	55	60	60	60
Ortho-phosphate (ppm)	0.20	0.10	0.10	0.15	0.18	0.20	0.25	0.20	0.10
Turbidity (JTU)	35	37	30	40	40	35	40	40	40
Apparent color (color units)	190	185	180	200	190	190	190	190	200
Temperature (C)	9.0	7.5	7.5	7.0	7.0	7.0	8.5	9.5	10.0
Water level (cm)	53	52	52	51	51	50	50	50	49



Table 5. *Physical and chemical constituents of the upper swamp of Tributary I over a 24 hour period 8-9 May 1969*

Time of day	1800	2100	2400	0300	0600	0900	1200	1500	1800
Dissolved oxygen (%)	80		76		71		76		80
Hydrogen ion	6.9	6.8	6.8	6.6	6.9	6.9	6.9	6.8	6.8
Total hardness (ppm)	50	50	50	52	53	60	55	50	50
Calcium hardness (ppm)	40	40	40	40	40	40	40	40	40
Total iron (ppm)	0.08	0.08	0.09	0.09	0.10	0.15	0.19	0.10	0.05
Alkalinity (ppm)	45	45	50	46	55	50	60	60	55
Ortho-phosphate (ppm)	0.10	0.05	0.01	0.05	0.10	0.18	0.13	0.10	0.10
Turbidity (JTU)	25	19	25	20	20	15	25	20	20
Apparent color (color units)	130	115	120	115	115	100	130	110	140
Temperature (C)	10.5	7.5	7.0	5.0	3.5	4.0	7.0	10.0	11.0
Water level (cm)	22	22	22	22	21	21	21	20	20



as seen in the April series. The fluctuations of apparent color and turbidity had no regular patterns.

Hardness and alkalinity values were higher for the May series because the water level was lower. Although no biotic influence appeared to be affecting hardness and alkalinity, these constituents exhibited a steady, although slight, increase throughout the 24 hour period. Dissolved oxygen steadily decreased during the period, showing an inverse relationship to the concentration of alkalinity. There was apparently no daily pattern for total iron or orthophosphate, although the latter increased from midnight through noon.

In Tributary 1, per cent saturation of dissolved oxygen appeared to exhibit a daily cycle, but this was a consequence of temperature; the actual concentration of dissolved oxygen remained fairly constant during the 24 hour period. Calcium hardness of Tributary 1 remained constant for the entire period; but total hardness (implying magnesium hardness) showed somewhat of a cycle, reaching a peak at 0900 hours.

In comparing the two 24 hour series, the major differences are with physical factors and were only in terms of absolute concentrations. For the May series, water level, turbidity, and apparent color had decreased, while temperatures were higher. Chemical constituents displayed the expected variations with water level. It is perhaps more significant that no striking dissimilarities were found between the two sampling dates in terms of chemical cycles, implying that the daily chemical patterns are not unique to the migration period.



## PREMIGRATION

This period is from the onset of ice formation, and thus minimum water temperatures in autumn, to the beginning of the nymphal migration at about the time of spring break-up of the river ice.

### Resumé of Physical and Chemical Conditions

Freeze-up first occurred in the swamp areas. By the end of October 1969, the upper swamp was covered with 5 cm of ice, but water in Tributary 1 continued to flow over the waterfall, under the ice. By the middle of November the tributary had ceased flowing, and by the end of February 1970, the water of the upper swamp was completely frozen into the substrate.

In the river the first ice was formed on the pools in late October, and by 23 November 1969, all of the riffles and pools were ice-covered. Water in shallow areas of pools and at the edges of riffles eventually froze into the substrate, thus eliminating these areas as a suitable habitat for most of the aquatic insects, including the nymphs of *L. cupida*. Because of the ice cover, by early spring less than 1% of the ambient light was penetrating through the ice (Figure 8), and by March 1970, this light had a considerably different spectral character in the water than was found in the ice-free season.

Spring break-up occurred at about the same time in both years, and, as witnessed in 1969, began by melt water flowing over the top of the river ice. At this time (6 March 1969) there were pools of water on top of the ice in the lower swamp, but this water was not yet running into the river. On this date the river water level was at 81 cm, but the migration of *L. cupida* had not yet started.





## The Premigration Population

In an effort to detect changes in the distribution of *L. cupida* nymphs during the ice-cover period, monthly samples were taken from the four habitats of the river study area (Figure 1). The macroinvertebrate community of the Bigoray River has been previously described by Clifford (1969) and the results of my sampling are in general agreement. Disparities are thought to be due mainly to the different sampling methods used and the different areas of the stream sampled (Appendix),

The results of the winter sampling are presented in Tables 6 and 7. *L. cupida* males are somewhat shorter than females of a comparable age (Clifford 1970). There appears to have been only slight growth of the nymphs through February (Table 6). The increase in size of both males and females in March might be due to a sampling error incurred by sampling a non-randomly distributed population or to immigration of large nymphs from other areas of the river. Length measurements are from rather small numbers, and do not correspond even in pattern to Clifford's analysis (1969 and 1970), where the nymphs were shown to have a uniform though very slow growth rate throughout the winter. The sex ratio of the population in winter was near unity, indicating a lack of differential habitat selection between males and females over the winter premigration period. Except for the December sample, there was little change in percentage numbers of *L. cupida* in the total stream fauna.

Table 7 shows the data of the premigration population when separated into the four river areas (RA, PA, RB, PB). Percentages in this table were calculated separately for each of the four habitat areas. For the entire winter period the major part of the *L. cupida* population was found in PA and RB.



Table 6. *Total lengths, numbers<sup>1</sup>, and per cent numbers<sup>2</sup> of male and female L. cupida nymphs from the Bigoray River during the premigration period.*

Date	Mean length of males (mm)	Mean length of females (mm)	Mean length of unsexed nymphs (mm)	Mean length of all nymphs (mm)	Per cent numbers
<u>1969</u>					
17 October	6.4 (52)	6.7 (44)	2.7 (7)	6.2 (103)	18.4
29 November	6.9 (21)	7.0 (23)	3.0 (1)	6.8 (45)	23.8
27 December	5.5 (16)	5.9 (11)	2.7 (2)	5.4 (29)	8.9
<u>1970</u>					
25 January	5.2 (27)	7.0 (21)		6.0 (48)	23.6
28 February	5.2 (18)	6.0 (22)	2.7 (7)	5.2 (47)	25.0
27 March	7.3 (17)	8.4 (17)		7.9 (34)	19.4

<sup>1</sup>Numbers are indicated in parentheses.

<sup>2</sup>Per cent numbers are calculated from the total stream fauna.



By January 1970 the *L. cupida* population had been reestablished to its previous October levels in PA, but remained at lower density in RB, and was practically eliminated from RA. The lower riffle (RA) was of fine gravel, while RB had a much coarser substrate, thus providing more potential habitats. During the ice-free period, all of the nymphs collected from RA were near the undercut west bank, and water of this area froze completely into the substrate during the winter, eliminating it as a habitat. Edge areas of RB were also frozen, but here nymphs were found in many of the midstream areas. Clifford (1969) suggested that nymphs concentrate in the pools during the winter, and this appears to be generally true for my study. In terms of the macroinvertebrate community of each area, Table 7 shows that the *L. cupida* population tended to become a larger percentage of the community in pool PA after ice formation. At the same time the percentage of *L. cupida* decreased in both riffles RA and RB.

### Summary

Premigratory data indicate that *L. cupida* undergoes very little growth in the winter, and that the population is apparently stable and not involved in any major movements during the winter—except perhaps those caused by elimination of habitats by ice. These movements are caused by ice exclusion of edge habitats and apparently occur soon after the river is completely ice-covered. During the winter the nymphs are in a cold, dark environment of limited autotrophic production, and it is likely that this situation has stress effects on the nymphs.



Table 7. *Total numbers and per cent numbers<sup>1</sup> of L. cupida nymphs from each habitat area of the Bigoray River during the premigration period.*

Date	1969			1970		
	17 Oct.	29 Nov.	27 Dec.	25 Jan.	28 Feb.	27 Mar.
<u>RA</u>						
Total numbers	5	11	0	3	0	1
Per cent numbers	1.4	16.7	0.0	4.2	0.0	2.0
<u>PA</u>						
Total numbers	32	2	14	32	25	29
Per cent numbers	41.5	22.2	28.0	52.4	58.1	48.3
<u>RB</u>						
Total numbers	66	28	8	15	13	4
Per cent numbers	50.4	27.2	4.4	23.8	21.3	8.2
<u>PB</u>						
Total numbers		4	7	0	9	0
Per cent numbers		36.4	25.9	0.0	17.6	0.00

<sup>1</sup>Per cent numbers are calculated from the macroinvertebrate community of each habitat area.





## MIGRATION

In early April both in 1969 and 1970 the upstream nymphal migration of *L. cupida* started during the high water period resulting from the spring break-up of ice on the Bigoray River. Physical and chemical conditions were recorded more frequently over these periods, and the results for the spring of 1969 are shown on expanded scales in Figures 11, 12 & 13 for the river and Figures 14 & 15 for Tributary 1.

### Resumé of Physical and Chemical Conditions

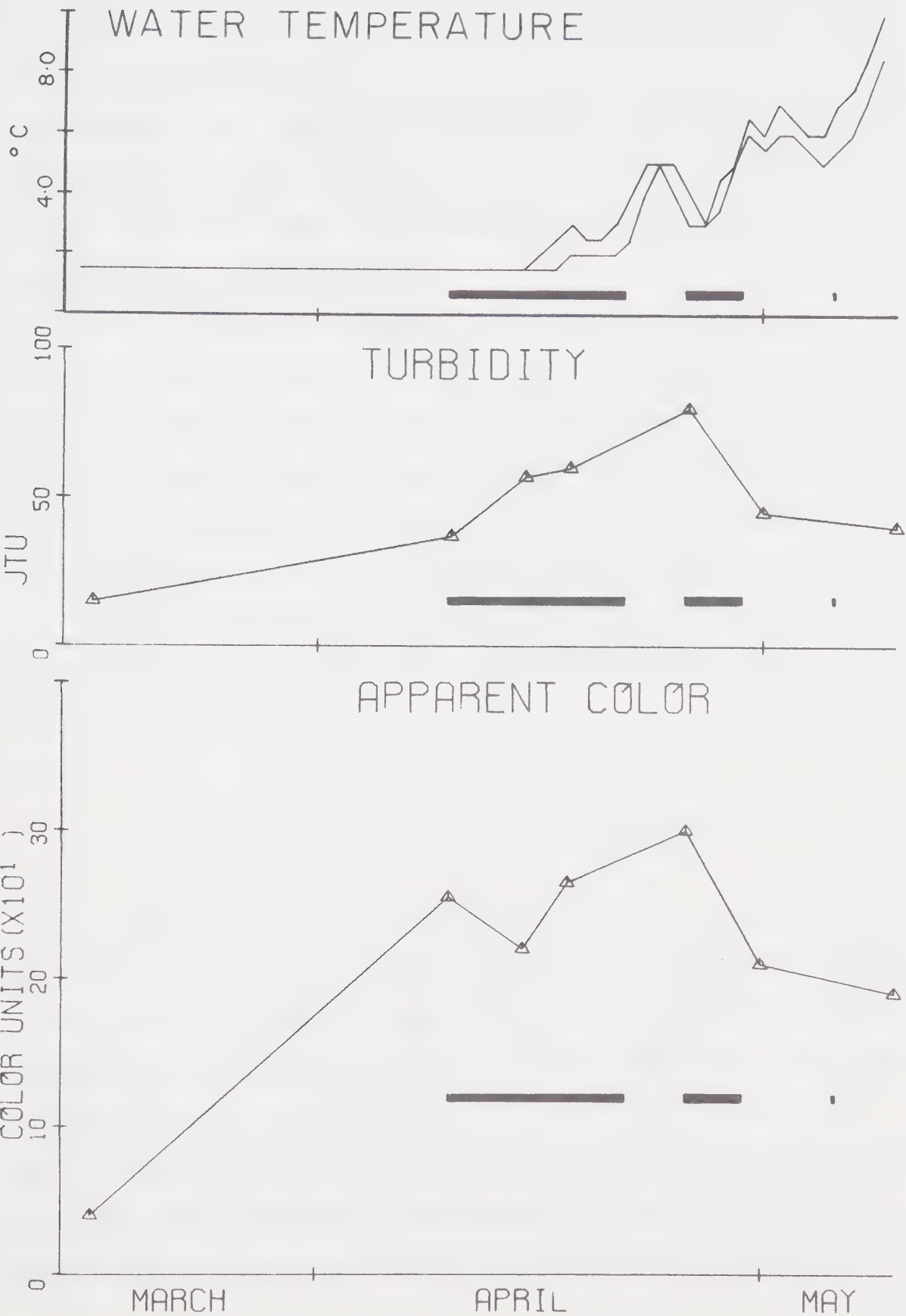
By the time of the spring break-up, the river water had become much more colored and turbid than during the winter (Figure 11). Water draining into the river from the tributaries was running over the solid ice of the muskeg and swamp areas. The mouth of Tributary 1 was spread over a wide area to the west of its normal outlet. As the ice in this area melted, all the water of Tributary 1 was channelled over the waterfall near the outlet of the tributary. During the run-off period in the spring of 1970 all discharge was over the waterfalls. At this time the tributary water was generally less colored and turbid than the river water.

On 9 April 1969, water temperature was 0 C at the outlets of all four tributaries. At this time the temperature of the river's surface water was 0.5 C. The Ryan thermograph, which was midstream in PA and about 1 meter deep, showed no daily variations until 16 April (Figure 11). However, temperatures at the river's edge, where the migration took place, showed a daily variation by 12 April, and probably were fluctuating before this date. These "edge" temperatures depended on the orientation of the sun and the current at the bank. Generally the water of the tributaries warmed more





Figure 11.      *Water temperatures, turbidity, and apparent color of the Bigoray River during the migration period of 1969.*  
Periods of migration are indicated by the black bars on each graph.





quickly and was subject to greater daily fluctuations than was the river, the exception being Tributary 4 which was always colder than the river during the migratory period.

During the early part of the break-up period, the level of the river was highest near midnight and lowest near noon, but later, when snow cover had diminished, water level fluctuations lost this pattern and were influenced mainly by precipitation.

Chemical conditions in the river were mainly influenced by the increased discharge (Figures 12 & 13). Bicarbonate alkalinity and hardness were at low levels. During the break-up, orthophosphate and total iron values were initially high, but soon returned to winter levels. There were only slight changes in pH during the break-up, but, of course, dissolved oxygen levels increased rapidly as the ice broke up.

The chemical characteristics of the tributary were much like those of the river, but with less dissolved and suspended materials (Figures 14 & 15). The tributary water tended to be slightly more acidic than the river.

### Description of Migration in the River

The migration was first observed on 9 April 1969. By this time the river water level had risen to 100 cm. Most of the winter's ice was still in place, under the water, but several thin ice areas had opened in the river, and water was surging up and down through these holes. The nymphs were moving upstream along the bank of the river, at the water's edge. When a tributary was encountered, they would move up the tributary channel. Usually the nymphs would stay in contact with the river bottom as they crawled upstream, but in quiet water regions they would swim by moving







Figure 12. *Total iron, dissolved oxygen, and hardness of the Bigoray River during the migration period of 1969.*  
Periods of migration are indicated by the black bars on each graph.

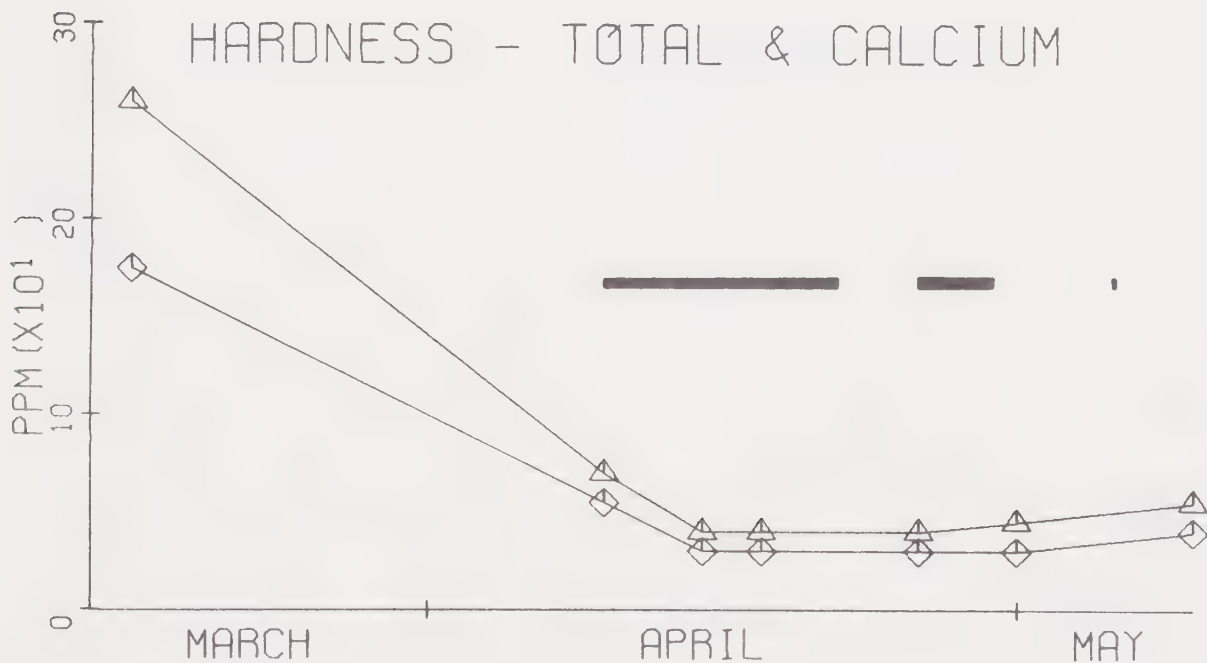
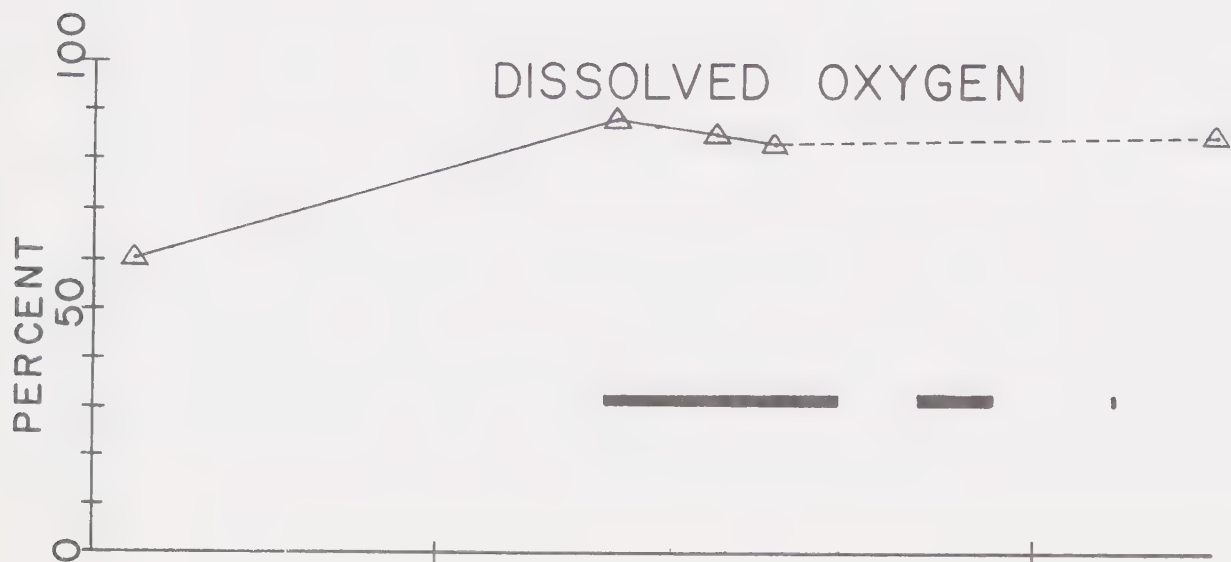
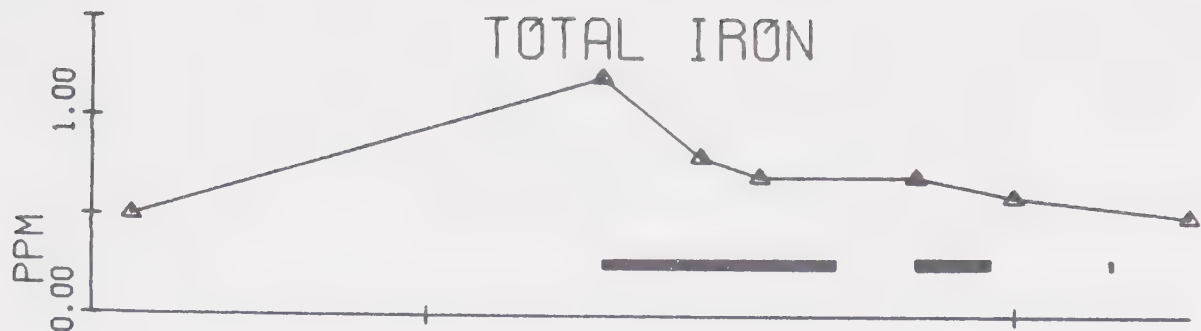






Figure 13. *Orthophosphate, hydrogen ion, and bicarbonate alkalinity of the Bigoray River during the migration period of 1969. Periods of migration are indicated by the black bars on each graph.*

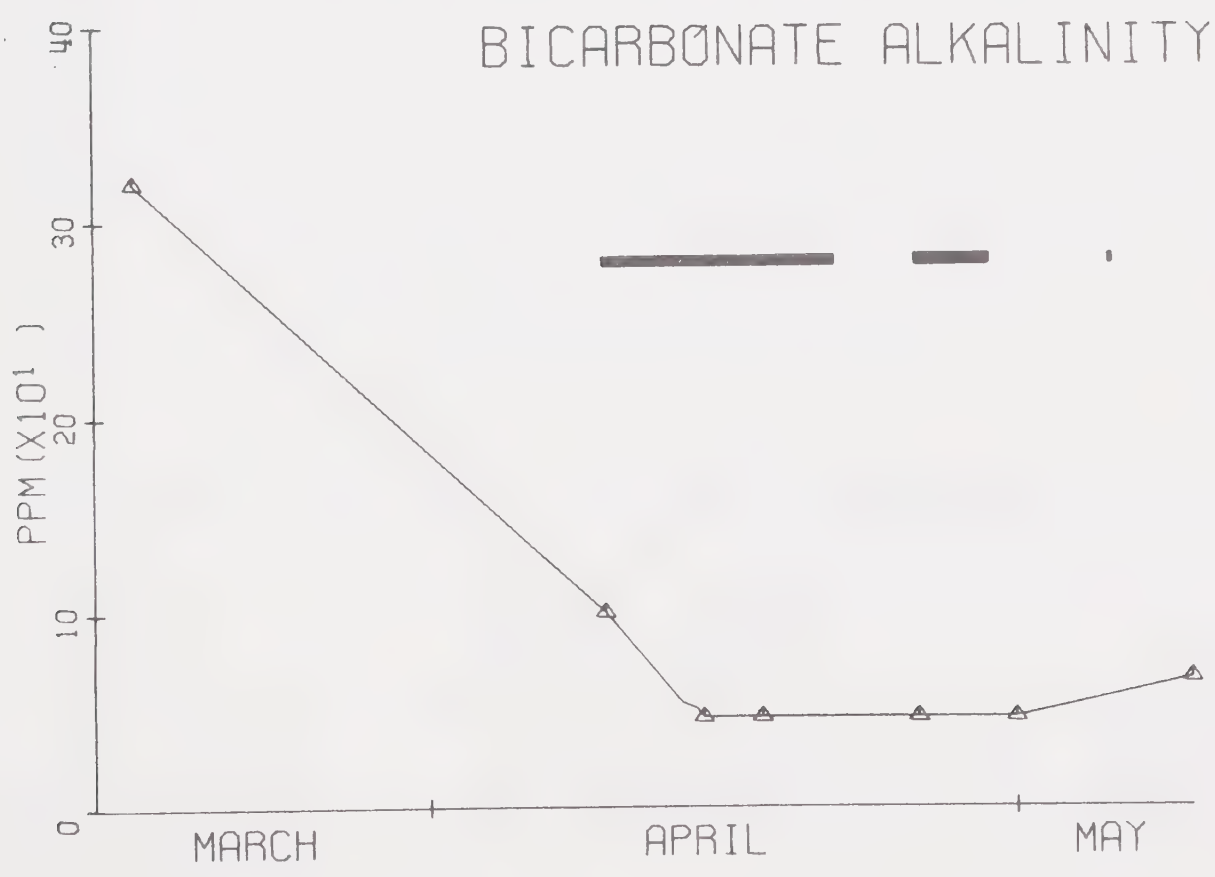
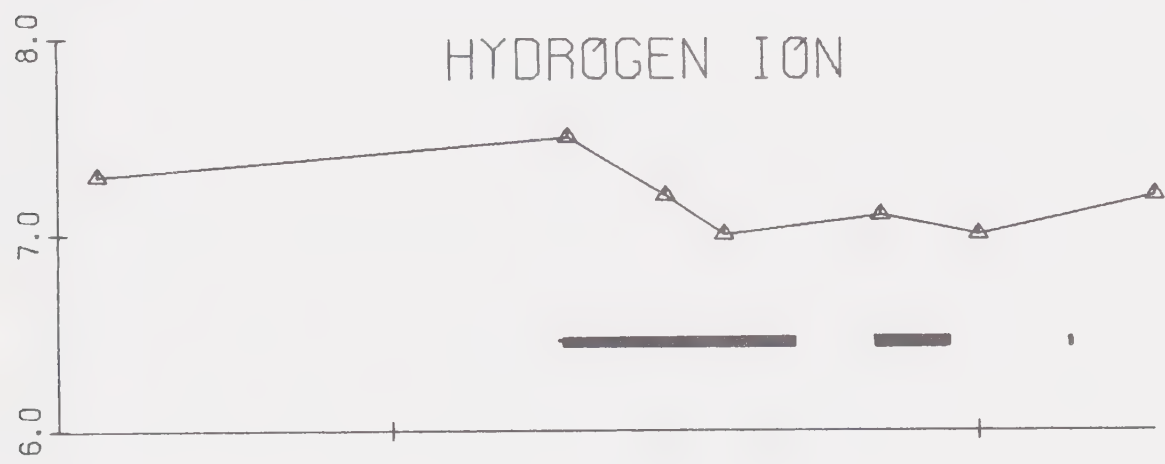
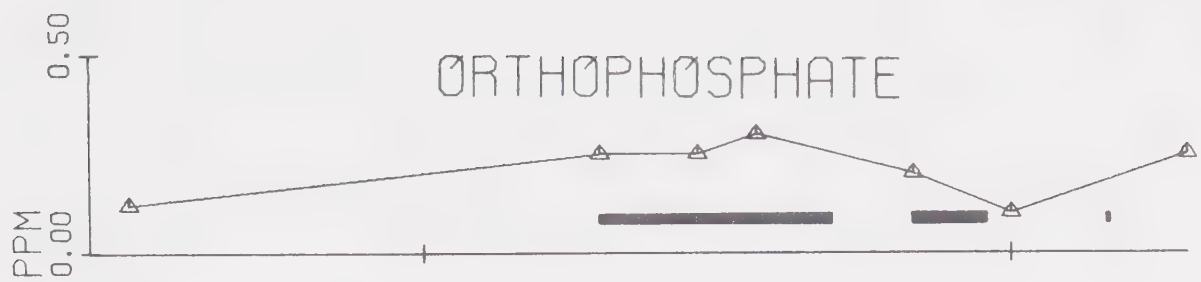








Figure 14.      *Water temperature, turbidity, apparent color, orthophosphate, and total iron of Tributary I water during the migration period of 1969.*

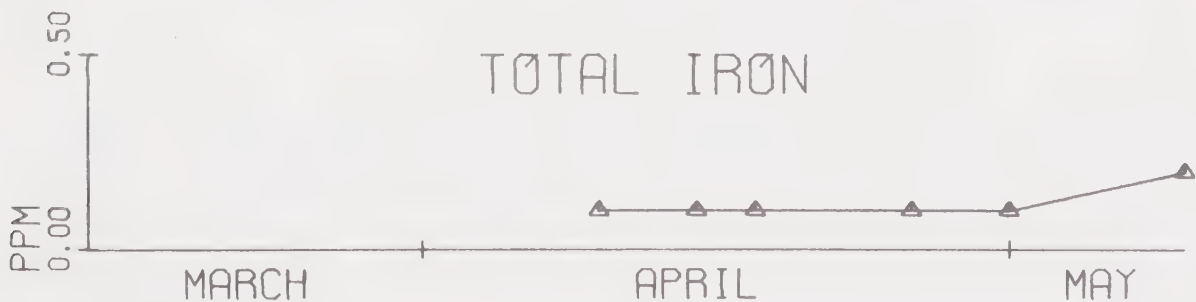
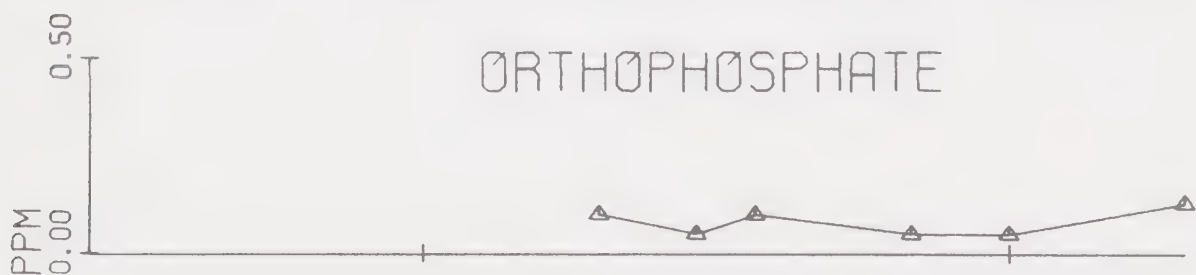
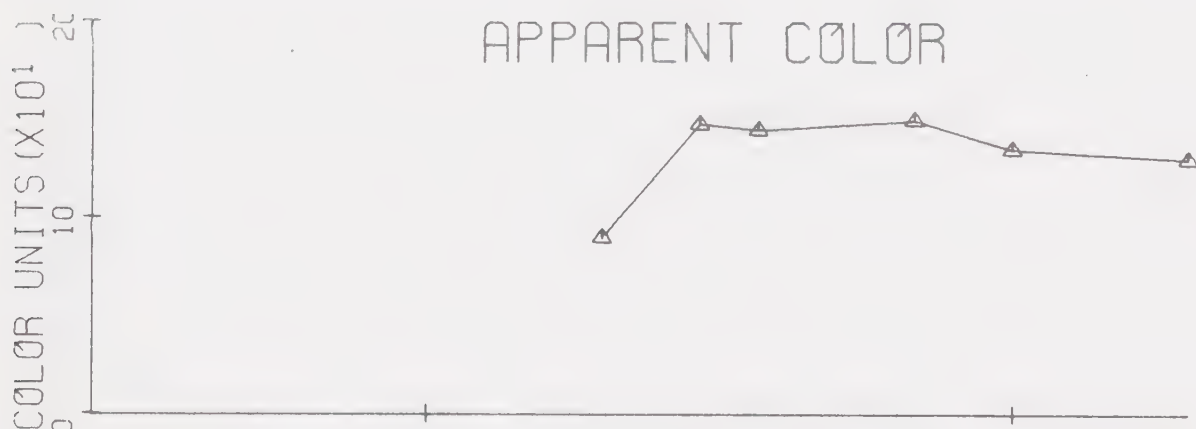
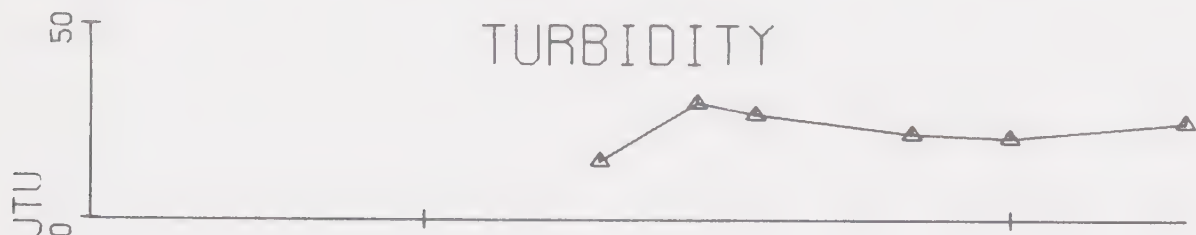
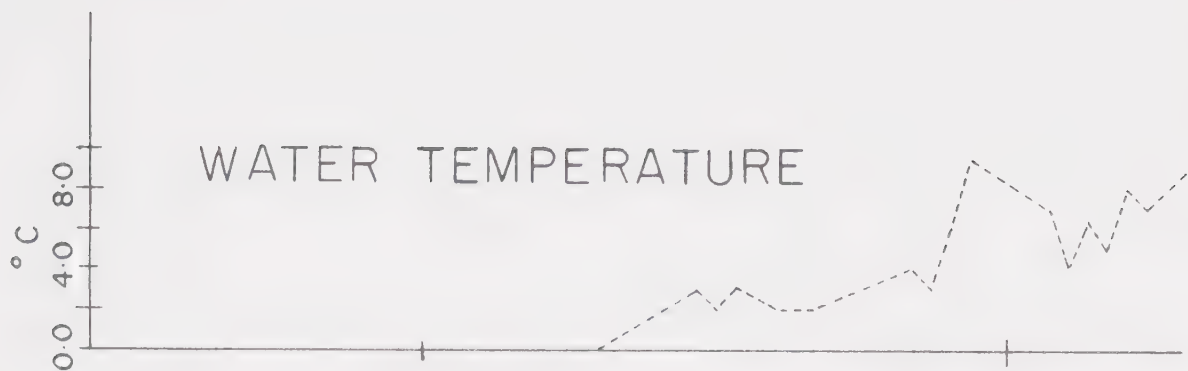
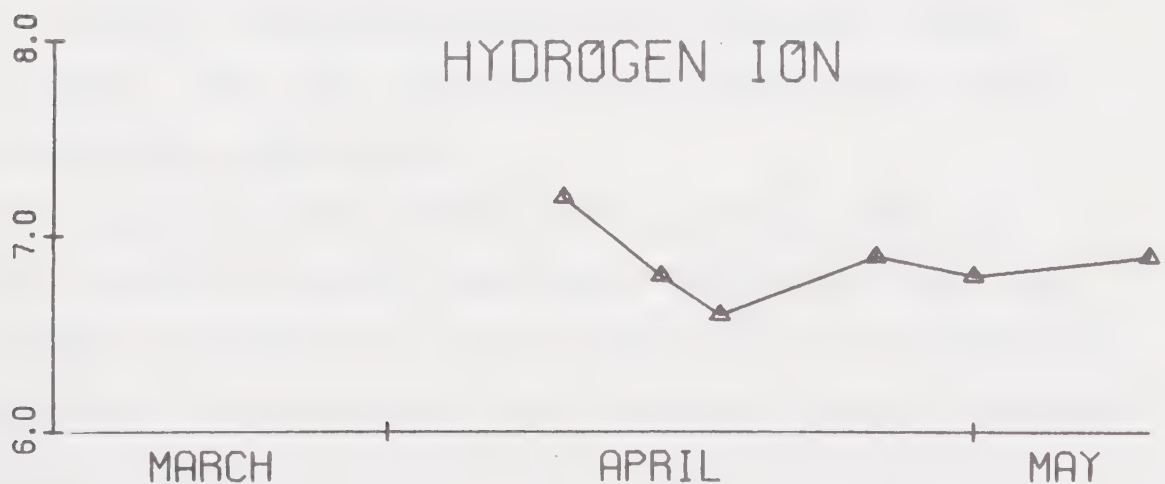
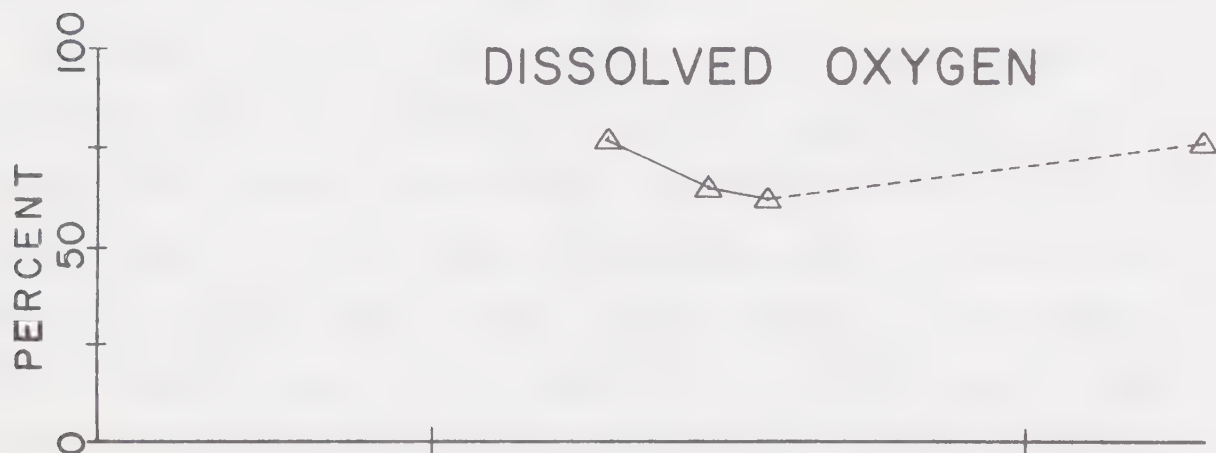
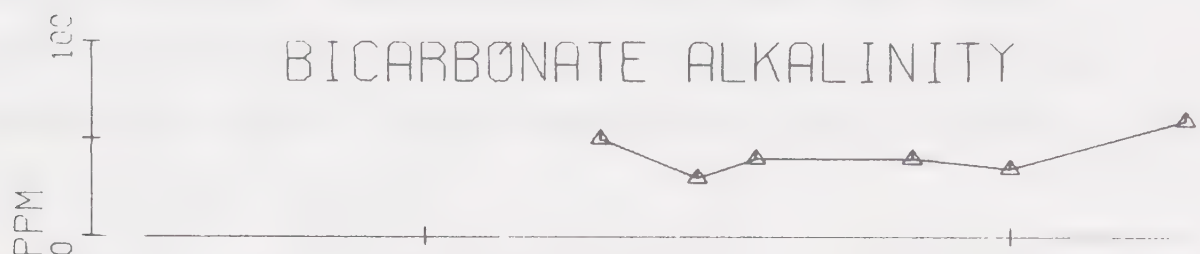
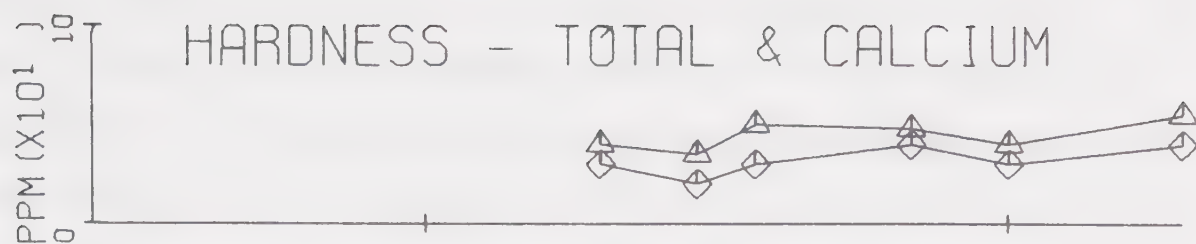






Figure 15.     *Hardness, bicarbonate alkalinity, dissolved oxygen,  
and hydrogen ion of Tributary I water during the  
migration period of 1969.*







their bodies in vertical wave-like undulations. Males and females of all sizes were observed migrating on both sides of the Bigoray River and along the entire river course mapped in Figure 1. In some areas it was impossible to see moving nymphs because of overhanging vegetation or newly formed surface ice but, by sampling with dip nets, nymphs were always found in these areas. Even in relatively quiet water areas several hundred meters downstream from the bridge, nymphs were observed moving upstream; hence migratory behavior appeared general for the entire *L. cupida* population of the river.

#### Initiation and Cessation of the River Migration

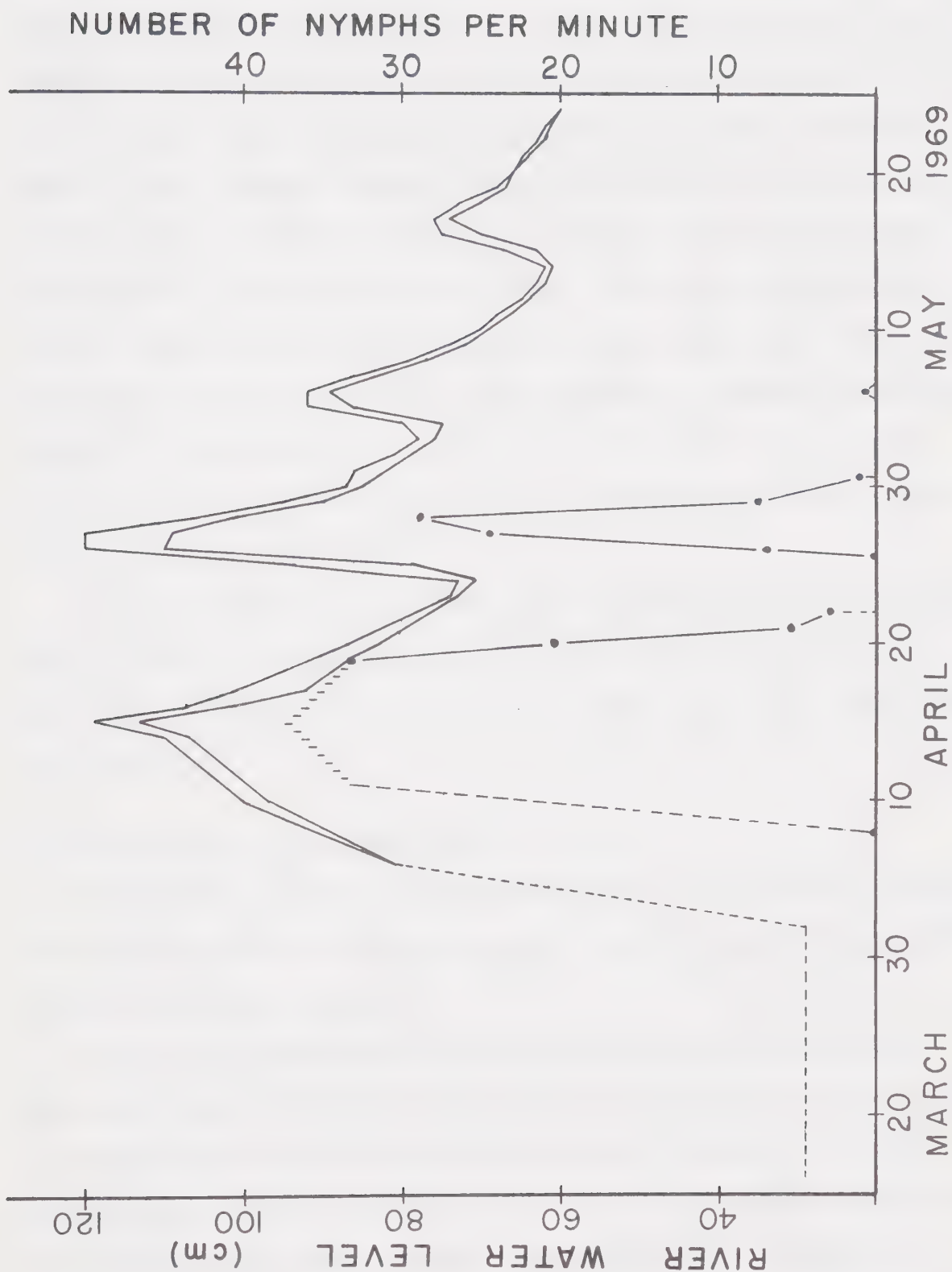
The water level of the river continued to rise to a high of 119 cm on 14 April (Figure 16). The numbers of migrating nymphs tapered off as the water level declined, and by 21 April, with the level at 76 cm, the migration ceased. Three days later rain and snow caused the river to rise again, and by 25 April when the water level had reached 98 cm the migration resumed. Migration ceased for the second time on 29 April, when the water level had dropped to 85 cm. On 5 May, following more snow and rain, the river rose for the third time, reaching 92 cm, and migratory activity resumed again. But on 6 May the water level had dropped below 90 cm and no more migrating nymphs were seen.

This sequence of events indicates that the initial stimulus for migratory behavior is related to some aspect of high water level. The chemical data of Figures 12 & 13 show no patterns that correlate with the nymphal migratory behavior pattern. And there are no apparent correlations between migration and the physical factors of Figure 11. Thus migration is closely associated with the physical aspect of water level fluctuation. It is felt that turbulence of the water during the ice break-up is a key





Figure 16. *Water level and numbers of nymphs migrating per minute in the Bigoray River 1969.* The upper two lines indicate daily maximum and minimum water levels. The lower line indicates nymphal migration activity (via nymphal counts). The broken line for water level indicates periods of no observations, and for migration, migratory activity that could not be accurately enumerated.





stimulating factor.

Migration ceased in the river when the water level dropped and turbulence (which was influenced by ice conditions in the river) was low enough for the nymphs to maintain themselves in their preferred habitats. These habitats were at the edges of pools where vegetation was growing from the river bottom or hanging into the water and on the river bottom in riffle areas. When the migration was waning in 1969, active nymphs were seen only in the riffle areas and not in the still water of pools. However, once the migration had ceased entirely, nymphs were never found at the edges of exposed riffles. Since current and turbulence would not be equal in all regions of the river at the same time, it is doubtful that migration ceased or started at exactly the same time in all regions of the river.

Of course nymphs that had moved into the drainage of the tributaries were in an entirely different habitat and, as will be discussed later, were subjected to a different sequence of stimuli from those nymphs still in the river.

#### Orientation and Direction of Movement

The upstream orientation and movement of *L. cupida* during migration is probably an effect of both the nymphs' shape and a behavioral response to water current by the nymphs.

Neave (1930) found that when even dead nymphs were subjected to water flow they always came to rest facing the direction of current. This was true regardless of the initial angle of the current to the nymphs. In 1969, when the level and edge turbulence of the river were greater than in 1970, migrating nymphs appeared to experience more confusion and difficulty in maintaining an upstream direction where back eddies were





produced along the river edges.

What is best termed a behavioral response to water current was seen during the 1970 migration when nymphs were observed climbing up through melt-holes around bank vegetation which had been frozen in the ice. As the nymphs were emerging through the holes into the thin layer of water covering the ice, they turned to face the current and, once free of the ice hole, began to crawl upstream against the current. The effect of the nymphs' shape on their orientation was also seen here, for those that were dislodged maintained their upstream orientation as they drifted back. As soon as they again contacted the ice substrate they began once more to migrate upstream.

#### Rates and Numbers of Nymphs Migrating

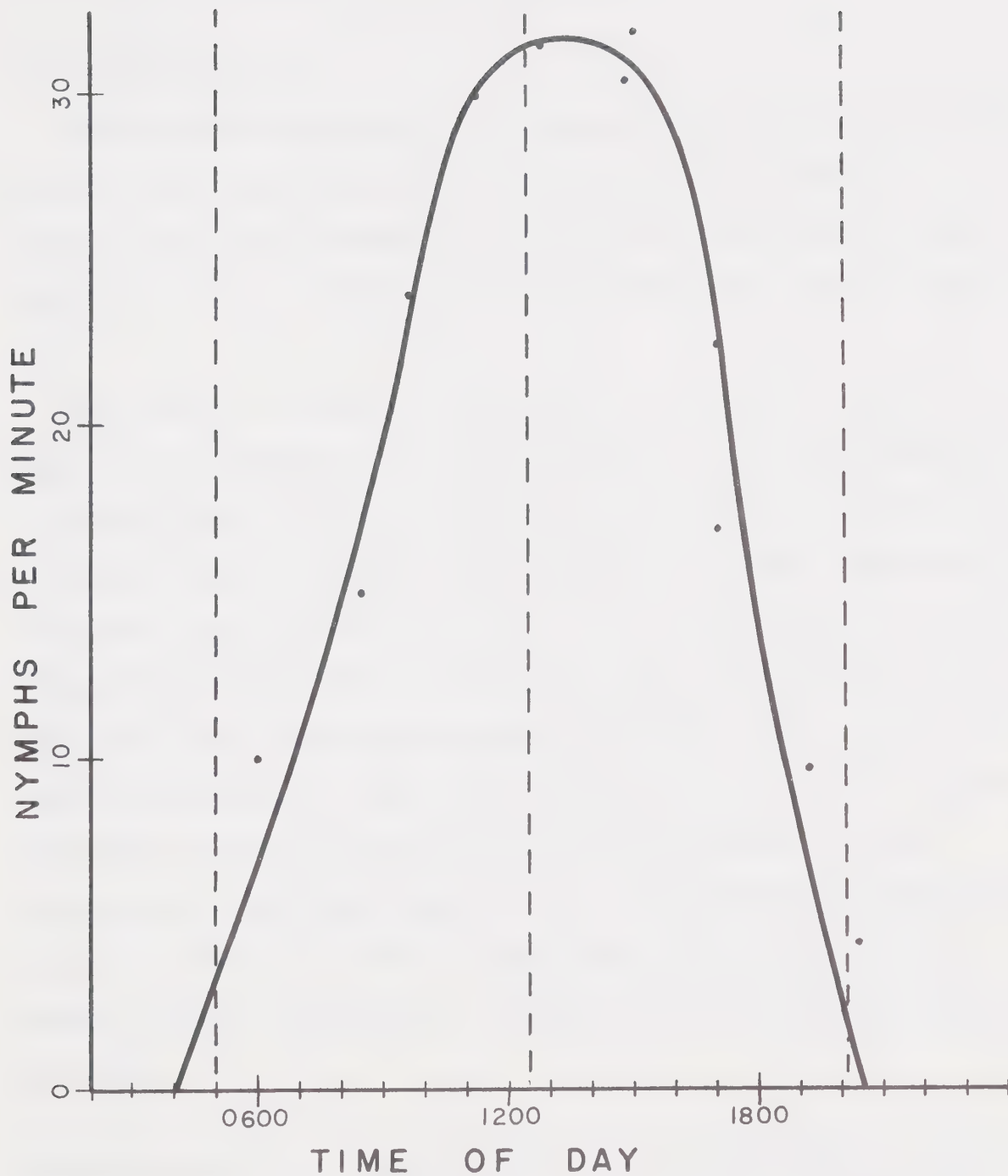
During the migration the nymphs were day active and the number of nymphs migrating during the day seemed to be primarily controlled by light intensity. Figure 17 shows this by a "best fit" curve drawn from counts of migrating nymphs as they moved across a line located between the bridge and the mouth of Tributary 1. Although other counting sites on the river displayed different daily patterns, movement at all sites was greatest near mid-day. The shape of the river bank might influence the characteristic activity curves at different count sites. The migrating animals were often densely congregated in quiet water along the stream banks early in the morning, suggesting that the water current and bank conditions along the river edges affected the overnight clumping.

Nymphs migrated at a rate of approximately 10 m/hour. By timing 28 nymphs, subjectively classed as small, medium, and large, the speed of each class was calculated to be 7.2 m/hour, 9.0 m/hour, and 18.8 m/hour respectively. Although nymphs were not timed during all hours of the day,





Figure 17. *Daily pattern of the number of nymphs migrating in the Bigoray River.* Points are the averages of ten one-minute counts of nymphs moving upstream over a line. Counts were made between the bridge and the mouth of Tributary 1, on 26, 27 & 28 April 1969. The broken lines indicate sunrise, solar noon, and sunset.





it appeared that their speed was uniform throughout the day. The faster rates of the larger nymphs appeared to be due to their greater size and not to greater activity or faster leg movement.

### Drift During Migration

Drift samples in the river were taken at 3 hour intervals over a 24 hour period on 16-17 April 1970, when the migration was taking place. Figure 18 shows that the greatest drift occurred between 1400 and 1600 hours; this period is similar to that of maximum numbers moving (Figure 17).

Net 1 was set on top of net 2 on the west side of the riffle (RA), while net 3 was placed on the east side of the riffle. The difference in the shape of the drift curves is due in part to different filtering rates of the drift nets, and probably to the difference in bank shape on each side of the river. The curve for net 1 is less in magnitude than net 2 because only 50 cm<sup>2</sup> of the filtering area of net 1 was submerged in the water. Net 2 was completely submerged (930 cm<sup>2</sup> of filtering area). The relatively small peak at 2400 hours corresponds to the typical *L. cupida* "behavioral drift"<sup>1</sup> pattern, which was subsequently found after the migration had stopped (see Figure 23; to be discussed in the Postmigration section). There were no obvious differences in the size of the drift animals over the 24 hour period. The sex ratio of the drifting nymphs was near unity.

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<sup>1</sup>*Behavioral drift* is a result of a diel behavioral characteristic with some orders of stream invertebrates. In the case of ephemeropterans, the greatest numbers of nymphs are found in this drift during the night hours.

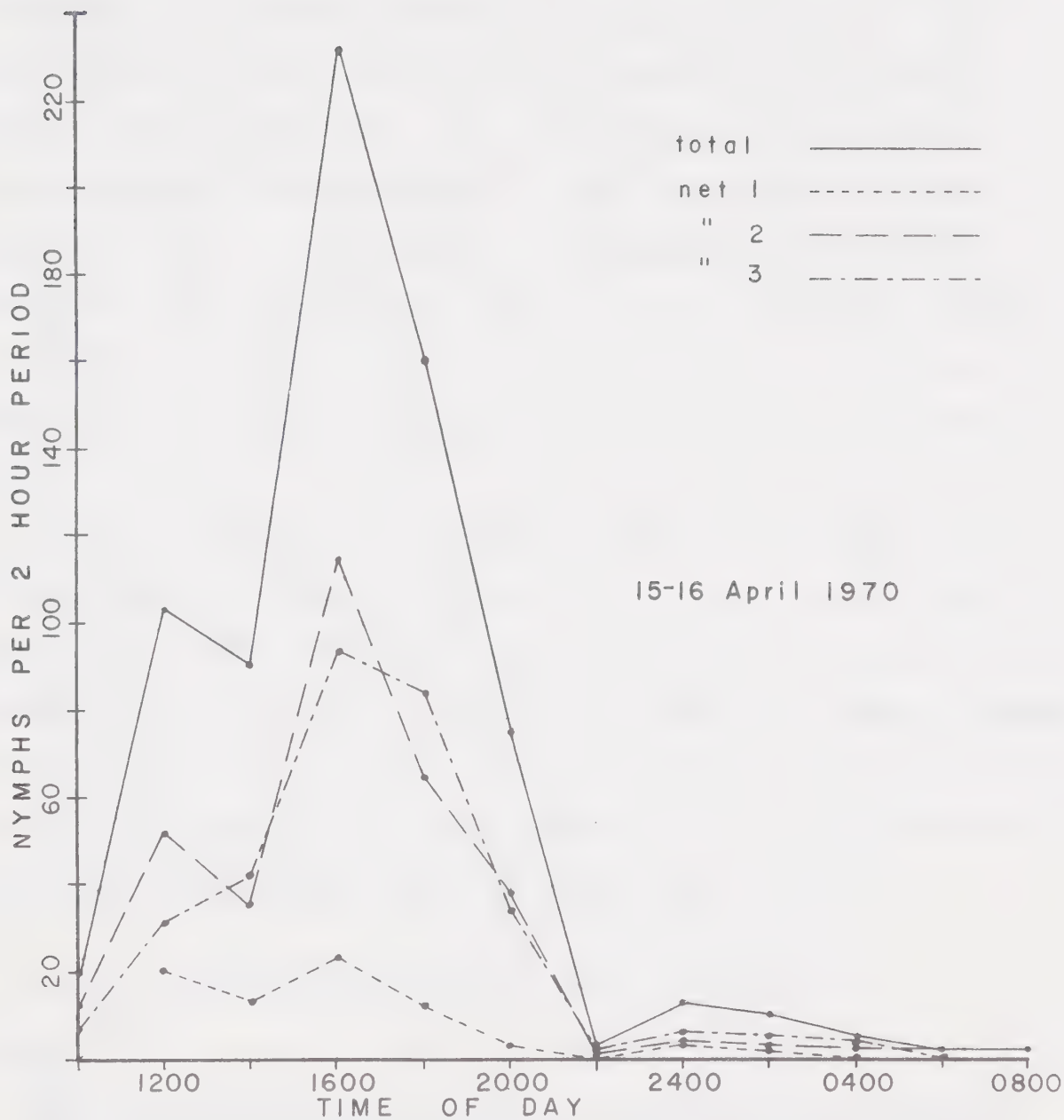
*Catastrophic drift* is the result of flooding and consequently has no diel pattern.







Figure 18. *L. cupida* stream drift as monitored in the lower riffle (RA) during the migration of I970. See text for explanation of curves.





## Gut Content Analysis

Gut contents were analyzed from *L. cupida* nymphs originally collected in the drift. The numbers of diatoms in the guts of nymphs of the same size were, as was found for drift activity, greatest during the 1400 to 1600 hour period (Figure 19b). There were not enough nymphs collected in the drift between 2000 and 0800 hours to justify an analysis for this time period. Hence it is not known if the apparent increase in feeding from 1800 to 2000 hours continued through the night. The similar patterns of graphs 17, 18 and 19b indicate that the nymphs fed at maximum rates during or just prior to the time period of greatest activity and maximum drift.

Figure 19a shows that in proportion to total nymphal volume, the guts of larger nymphs contained more diatoms than did those of smaller sized nymphs. Brown (1961) also found this phenomenon for *Baetis rhodani* (Pictet). My results indicate a probably change in the feeding habits between different size classes of *L. cupida* nymphs. The decline in diatom numbers for the 10 mm nymphs is unexplained. In my study there were no obvious differences between the feeding habits of male and female nymphs.

## Description of Migration in the Tributary

### General

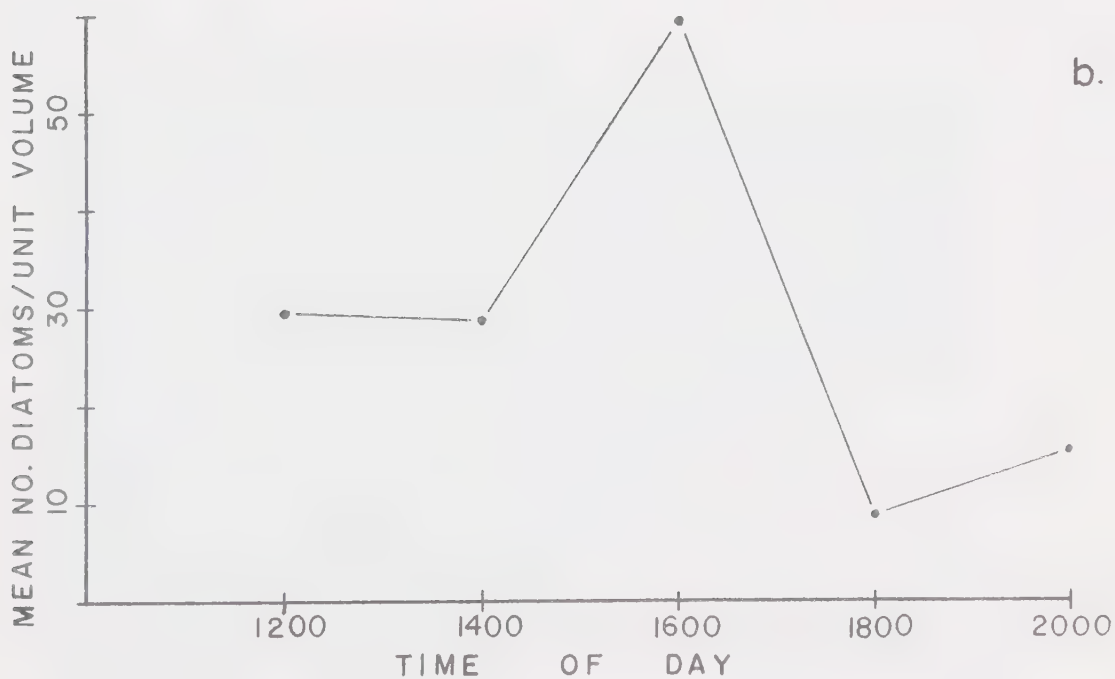
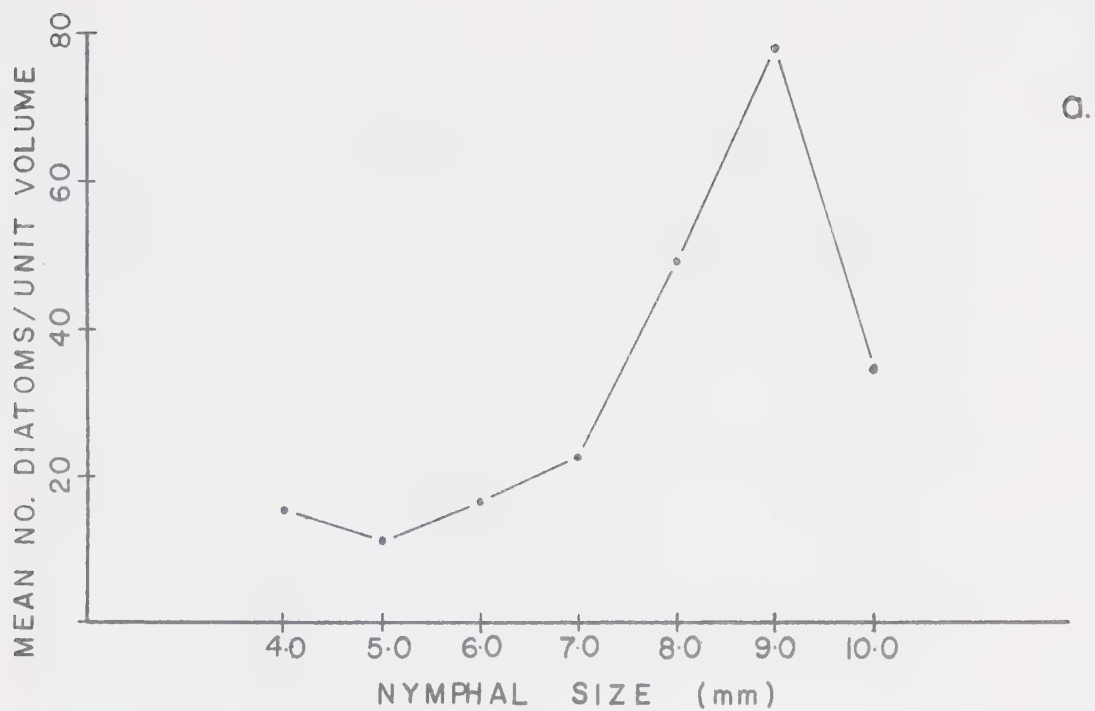
When the migrating nymphs encountered a tributary, they continued to follow the contour of the stream bank (which would lead into the tributary) and hence moved up the tributary and into the swamp and muskeg areas away from the river (Figure 20). The movement into the tributaries appeared to be the natural consequence of the upstream movement of the nymphs along the water's edge. All of the thawed tributaries (i.e., those connected by







- Figure 19.
- a. *Mean numbers of diatoms in different size classes of L. cupida nymphs. Each point represents from 5 to 25 nymphs collected from different time periods.*
  - b. *Mean numbers of diatoms in equally size-proportioned groups of 16 L. cupida nymphs at different times of the day. All nymphs were collected from the drift samples of 15-16 April 1970. Unit Volume is the volume of the nymph, roughly calculated as the cube of each nymph's total length.*







- Figure 20.
- a. *Tributary I as it flows into the Bigoray River.*  
Photo was taken during migration, 14 April 1970,  
from the bridge looking west.
  - b. *L. cupida nymphs migrating out of the Bigoray River  
into Tributary I.* Nymphs are moving from upper  
right to lower left, against the water current of  
Tributary 1. Photo was taken facing west in the  
area indicated in Figure 20a.





water to the river) were utilized by the nymphs, and each tributary had its own physical-chemical character. During early periods of the migration, the ice conditions of the river were such as to detour nymphs away from the outlets of some of the tributaries, but the nymphs were still exposed to the chemical and temperature conditions of these waters. In these cases there was no extra effort made by the nymphs to enter the "blocked" tributaries. There was no indication that any factor, other than the shape of the shore line, influenced movement out of the river.

Certainly temperature did not appear to play any role in influencing the nymphs to enter tributaries. Tributary 4 was always colder than the river during the migration, while the other tributaries were usually warmer than the river; yet *L. cupida* migrated as readily into Tributary 4 as into any of the other tributaries.

The first nymphs to enter Tributary 1 continued to move southward, up the drainage of the tributary, to the top of the hydrographic divide separating the north and south forks of the Bigoray River, some 1200 meters from the river. Although standing water from snow-melt connected the two watersheds for a time, the nymphs from the north fork never moved into the south fork drainage. Later during the migration when the substrate of the upper swamp had thawed, nymphs did not continue through it toward the ditch to the south.

Some mortality was suffered by the population during the migration due to the freezing of nymphs into ice which formed during the night. This situation was observed in both 1969 and 1970 at the outlet of Tributary 1, and these nymphs were found not to survive this freezing.

Apparently the boundaries of the migration pathway were formed in part by abrupt chemical gradients in the drainage of Tributary 1. Nymphs





were never found in the western part of the upper swamp, although all physical conditions there were comparable to the inhabited areas of this swamp. A comparison of water from these two areas revealed hardness values to be much greater in the uninhabited zone to the west. This abrupt chemical gradient probably acted as a barrier to migratory movement.

Tributary temperature had no discernible effect on the direction or extent of the migration. Along the migration path the water was always colder in areas 400 meters and 650 meters from the river than in areas north, south, or between these distances. But nymphs readily moved through these colder areas.

#### Rates of Movement and Daily Activity

The leading edge of the 1969 migrating nymphal population was located, beginning with the first observations on 9 April. Discharge of Tributary 1 was flowing over the ice at the waterfall, which nymphs were ascending by climbing up the vertical faces of ice on either side of the water pouring over the falls. Later, when the ice had melted away, the nymphs negotiated the waterfall by climbing up blades of grass hanging over the edges.

By the afternoon of 9 April the front of the migrating population in the tributary was 58 meters south of the river. Considering the average nymphal speed, it seems likely that the migration from the river had begun no earlier than the day before, 8 April. On 14 April the front of the migrating population was 650 meters south of the river; on 15 April the front was 750 meters south of the river.

If the duration of the daily migratory period in the tributary was the same as in the river (17 hours/day), and the few counts made in the ditch suggest it was, the rate of movement appeared much less (6 m/hour) in the rapid water of the ditch (see Figure 1) than in the river. If the



tributary migration did in fact begin on 8 April, the first nymphs, at a rate of 10 m/hour (see page 52) for 17 hours a day, could have moved 1360 meters south from the river by 15 April, assuming they were moving in a straight line. But, in fact, they had travelled only 750 meters. From the south end of the upper swamp (200 meters from the river) to the lower end of the ditch (420 meters from the river) there were no definite channels or waterways for nymphal movement. Instead, this area was replete with sedge and moss hummocks, and this would cause the migratory route to be anything but a straight path through this area. Also, the lack of an obvious water current to orient the nymphs could have contributed to a lengthy, more or less meandering migration course.

However, when the diurnal activity pattern of the migrating population is examined the problem appears more complex. If the threshold light intensity for activity were the same for all members of the population and all habitats uniformly illuminated, the daily activity pattern would be represented by a rectangle of the same height as the maximum amplitude of the actual activity curve (Figure 17) and a width equal to the maximum duration of that curve (i.e., 17 hours/day). Accordingly, at a rate of 10 m/hour for 17 hours/day the population could move 170 m/day.

As shown in Figure 17, however, the daily activity pattern occurring in the field was a bell-shaped curve. My field observations indicated that the nymphs' hourly rate of movement was the same for all hours of the daily activity period; thus this curve is probably the result of individual differences in the threshold intensity for migratory activity. There is no direct evidence that all nymphs moved for the same number of hours per day; however, the area under the curve in Figure 17 represents the total migratory activity of the population with regard to numbers and duration



during the day. This area has been calculated to be 59% of the rectangular pattern described in the previous paragraph. From this percentage two things can be derived: firstly, the population would move 59% of 170 meters/day, i.e., 100 meters/day; secondly, an individual would move *on average* for 59% of 17 hours/day, i.e., 10 hours/day. At the measured rate of 10 meters/hour, the latter would give 100 meters/day.

Between 13 and 14 April, and 14 and 15 April 1969, the front of the migrating population was found to have advanced approximately 100 meters each day up the drainage of Tributary 1. Similarly, from the start of migration in Tributary 1 (8 April) through 15 April, the nymphal population had moved approximately 750 meters from the river, an average of 94 meters/day. Hence a close correlation is found between calculated daily distances moved and those determined by locating the front of the migrating population in the field.

### Consequences of the Migration

The average total length of individuals of the *L. cupida* river population decreased as the nymphs moved into the tributaries (Figure 21a). This is the result of larger nymphs being able to move faster than smaller nymphs, thus enabling proportionately more of the larger nymphs to move into the tributaries during the migration.

At the southern extent of Tributary 1 (the furthest point of migration from the river) the nymphs were larger, and there were more females than males. This separation of sexes and sizes in Tributary 1 occurred in both years (Figures 21b & 21c), and would be expected since the females are larger than males of a comparable age, and larger nymphs moved at a faster rate.

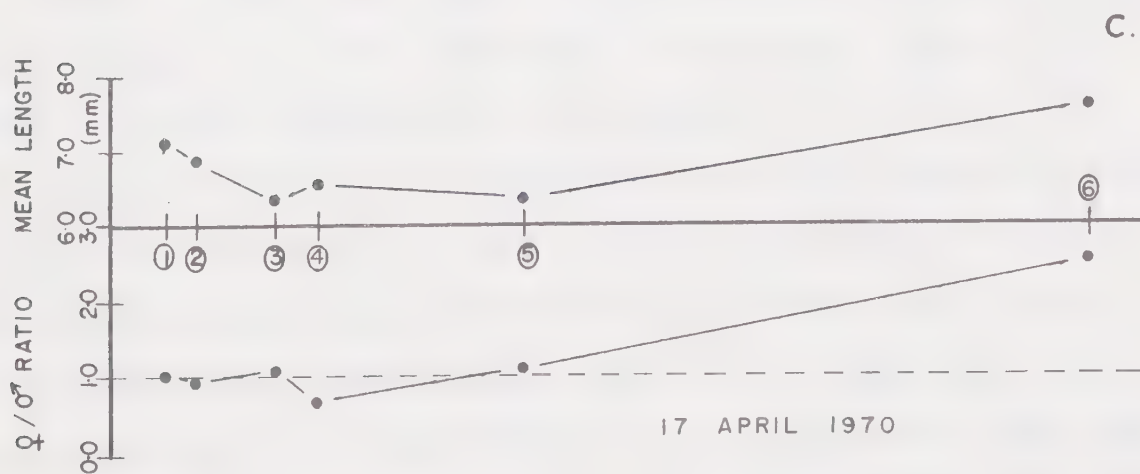
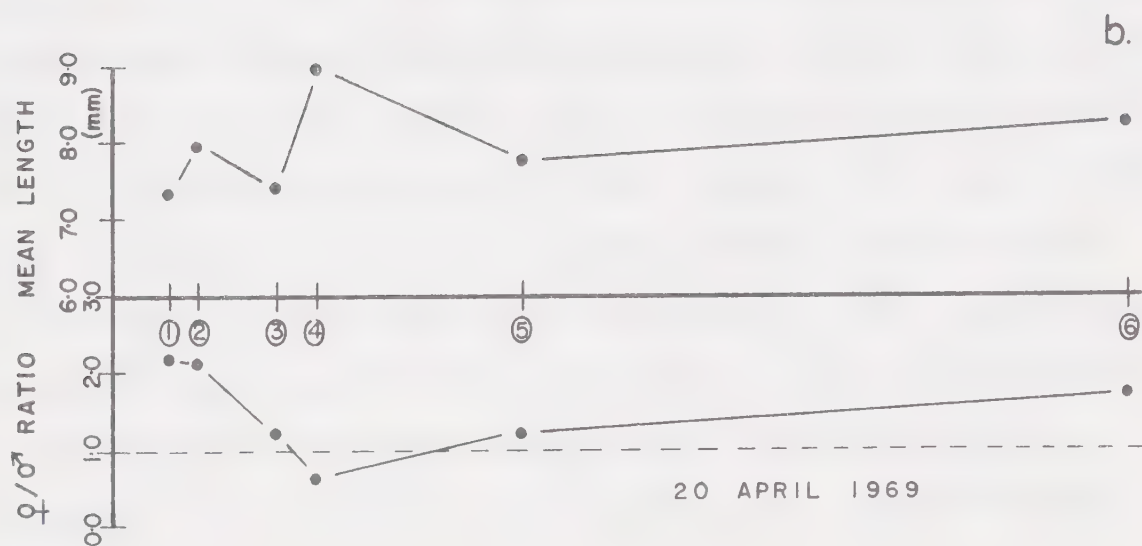
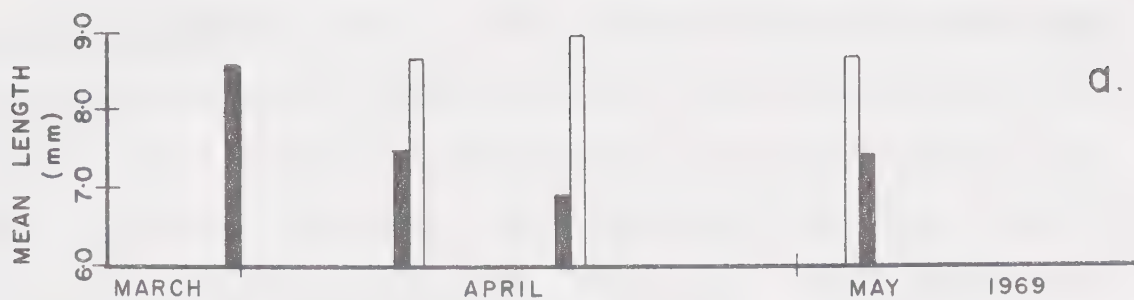








- Figure 21.
- a. *Mean total length of L. cupida nymphs in the Bigoray River (solid bars) and in Tributary I (open bars) during the migration period 1969.*
  - b. *Mean length and sex ratio of L. cupida nymphs along the drainage gradient of Tributary I during the migration 1969. 1, Bigoray River just below the mouth of Tributary 1; 2, top of waterfall of Tributary 1; 3, between lower and upper swamp; 4, in the upper swamp; 5, at lower end of ditch; 6, at southern extent of migration in Tributary 1.*
  - c. *Mean length and sex ratio of L. cupida nymphs along the drainage gradient of Tributary I during the migration 1970.*





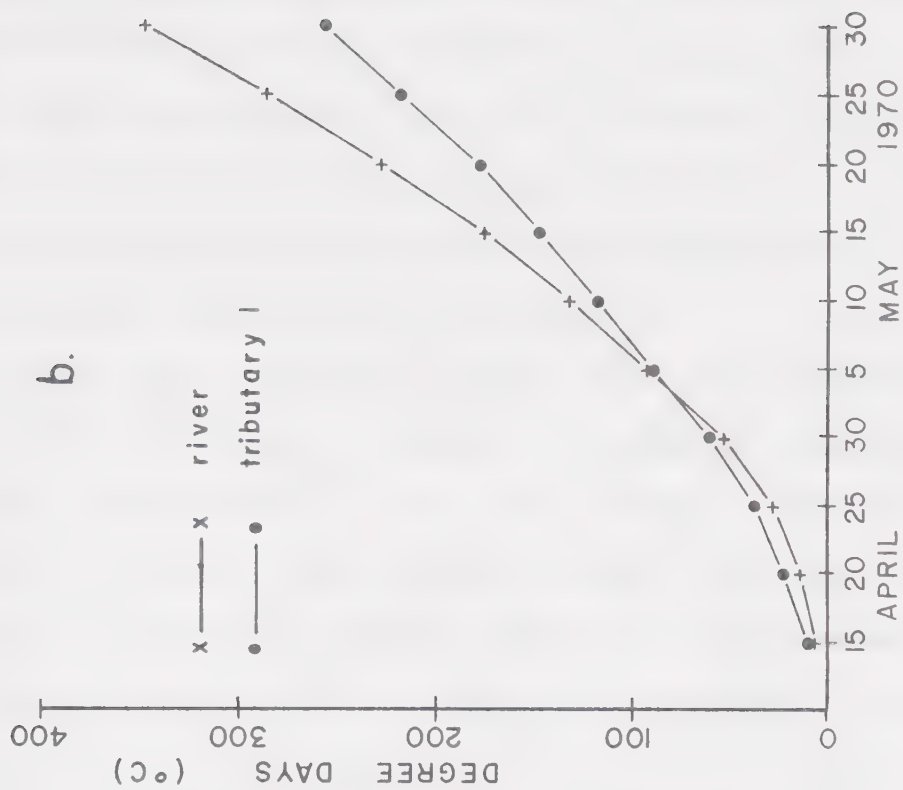
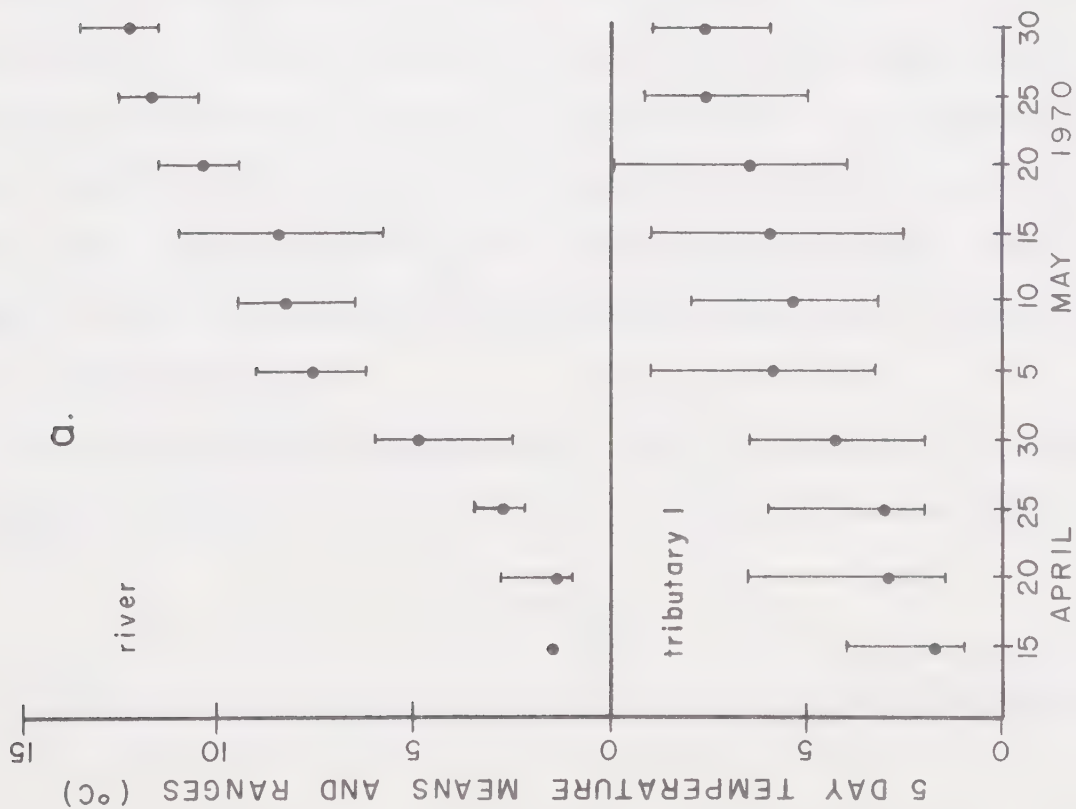
In late March 1969, before migration, the *L. cupida* population of the river was estimated to comprise 30% of the total macroinvertebrate fauna (excluding chironomids); in late March 1970, also before migration, this figure was 19%. By the end of the migration, 5 May 1969 and 3 May 1970, the *L. cupida* population in both years was estimated to comprise about 4% of the total macroinvertebrate fauna of the river. These figures give very little indication of the intensity of migration for either 1969 or 1970, since a great many of the migrants that entered the tributaries initially came from areas downstream from the river sampling sites. These data do indicate that the migration significantly decreased the number of nymphs in the river and, as shown before, influenced the average length of *L. cupida* nymphs remaining in the river. Because of the longer run-off period and higher water level, the migration was more intense in 1969. More tributaries were also available to the nymphs in 1969. Consequently more nymphs were able to move out of the river. By the end of migration in 1969 there were an estimated 605,000 nymphs in the upper swamp of Tributary 1. For the same area in 1970 there were an estimated 541,000 nymphs.

Figure 22 shows that during the first half month following the start of the spring run-off, water temperatures increased more rapidly in the swamp. After this initial period, 5-day means were higher in the river, even though the daily range of temperatures was always greater in the swamp. Consequently, 20 days after the start of the spring break-up, the river had accumulated more degree days than the upper swamp. These thermal conditions probably affected nymphal growth, and one might expect growth to be more rapid in the swamp during the first 2 weeks after spring break-up, but greater in the river thereafter. From 17 April 1970 to 3 May 1970,





- Figure 22.
- a. *5 day means and ranges of water temperature in the Bigoray River and Tributary I, 13 April through 2 June 1970.*
  - b. *Degree days as accumulated in the Bigoray River and Tributary I. Degree days are calculated by progressively summing average daily temperatures from 13 April through 2 June 1970.*







mean lengths of nymphs increased from 6.6 mm to 7.8 mm (an increase of 1.2 mm) in the upper swamp. For the period 15-16 April 1970 to 1-2 May 1970, the mean length of nymphs in the river, collected in the drift, increased from 6.2 mm to 7.0 mm (an increase of 0.8 mm). A comparison of growth after this early period could not be made because of the small numbers of nymphs collected in the river samples.

The type of food available to the river population in winter is different from that of summer. Qualitative assessment of gut content showed that *L. cupida* fed on a wider variety of food, especially detritus, in the winter. However, during migration the main item of the nymphal diet was diatoms. To compare the standing crop of periphytic diatoms in the upper swamp and the river during and following the migratory period, plexiglas plates were suspended in both areas on 14 April 1970 and withdrawn at intervals between 22 April and 1 June 1970 (Table 8). During the migratory period, the standing crop of periphytic diatoms was about twice as large in the upper swamp as in the river, although it was at low levels in both habitats. However, during the first half of May, the standing crop increased greatly in the river; diatom abundance in the river was nearly 100 times greater than in Tributary 1 at this time. Hence it is unlikely that the emigrant nymphs from the river would, as Neave (1930) suggested, enjoy the benefit of a more plentiful food supply for much more than a couple of weeks.

The main advantage of migration from the river seems to be in finding a habitat not subject to the uncertainties of great water level fluctuations.

### Discussion

I concluded in the preceding section that the initiation of migration



Table 8. *Relative abundance<sup>1</sup> of periphytic diatoms on 100 cm<sup>2</sup> of plexiglas plates introduced into the Bigoray River and upper swamp of Tributary I on 14 April 1970.*

Date withdrawn	River	Upper swamp
22 April	10	20
30 April	26	73
12 May	343 X 10	121
1 June	164 X 10 <sup>2</sup>	196

<sup>1</sup>The numbers represent the number of diatom cells counted in 4 strips of a Sedgewick-Rafter cell at 100X. They indicate only the relative abundance of diatom cells between the two habitats or in the same habitat on different dates.



was somehow affected by increased water velocity and turbulence. First I will examine other possible stimuli and then discuss the effects of velocity and turbulence.

Although the concentration of certain chemical constituents changed greatly during the spring break-up, the changes did not correlate well with the start and termination of the migrations. Nymphs moved into many tributaries, and these tributaries differed from one another in their chemical characteristics. Furthermore, *L. cupida* migrations have been reported from widely separated geographical regions of North America (Traver 1925, Neave 1930, Prater 1969).

There was no apparent correlation between photoperiod, intensity and quality of underwater light, and the three migrations of 1969. Photoperiod, of course, showed a uniform daily increase throughout the period in contrast to the discontinuous sequence of the three migrations during April and early May in 1969. Therefore, though photoperiod may have acted as a conditioning factor which made the nymphs susceptible to a later occurring proximal stimulus, it did not initiate the migratory sequence. Although the intensity and quality of underwater light changed during the spring break-up, there was no apparent correlation between these changes and nymphal behavior. Light intensity greatly increased when the ice broke up, but Neave (1930) reported a situation in which *L. cupida* nymphs moved up a roadside ditch, out of Lake Winnipeg, at a time when the lake was still ice-covered.

Water temperature would seem a likely trigger for nymphal migration (Allee and Stein 1918, Moon 1940), but there is no evidence of this for the Bigoray River migrations. The wide range of temperatures in Tributary 1 through which the nymphs moved also indicates a lack of thermal influence





on migratory stimulation.

The two remaining factors related to changing water level in the Bigoray River are water velocity and turbulence. These two factors are so closely related that they require consideration together. It seems best to discuss first the character of each and then discuss how the two factors are related.

It is well known that water velocity is not uniform at all cross-sectional points of a stream; instead, the zones nearer the stream bottom and banks exhibit less velocity. The situation becomes much more complex when a meandering stream with alternate pool and riffle areas is considered. In slow current areas, such as pools, precise estimates of water velocity are difficult to make because most measuring methods are not accurate at very low velocities.

Turbulence, simply defined, is the disruption of laminar flow with water currents moving in lateral and vertical directions. Turbulent flow is the only type of flow in natural running waters; but as yet there is no accurate way to measure this phenomenon. It is known, however, that turbulence increases in a general linear fashion with velocity.

Velocity and turbulence are greatly increased in the Bigoray River during the spring break-up. These factors in turn would cause a greater bed load, and this is indicated by the high turbidity values during the spring break-up. The actual flow patterns of the river are much more complex during this time, since the river is both an open system (run-off water on top of the winter's ice) and a closed system (water in the under-ice channel). Flow patterns during the spring break-up are further complicated by holes appearing in the ice cover, through which the water can boil up. Furthermore, as the ice eroded in the spring, cup-like





excavations, from 5 to 15 cm wide and 3 to 8 cm deep, were seen in the undersurface of the ice (the top surface of the ice was still relatively smooth). These depressions were caused by turbulence during break-up, and they in turn tended to create additional turbulence.

*L. cupida* is known as a "clinging" species (Needham, Traver and Hsu 1935), being found on emergent vegetation or allocthonous vegetation, on which the nymphs graze for periphytic and detrital material. The nymphs' winter habitat is restricted by edge water freezing into the substrate, and this accounts for the nymphs congregating in pools and less turbulent areas of riffles. Since much of the population will be "out of place" at the time of the spring break-up, the nymphs would be more susceptible to the effects of increased water velocity and turbulence.

I believe it is water velocity and turbulence that initially stimulate the migratory behavior of *L. cupida*. The correlation between water level and migration activity supports this conclusion, as does the apparent lack of upstream movement of nymphs prior to the spring break-up. As water level dropped, and velocity and turbulence decreased in the river, the nymphs would have experienced less stress and the river habitats would have again become suitable and hence migration would have ceased. In the tributaries, migratory movement also ended when a suitable habitat was found, but here it was not so much a result of decreased turbulence as it was a thawed substrate at a sufficient depth.

A velocity-turbulence stimulation of migratory behavior seems equally applicable in all reported cases of *L. cupida* migration. In all areas where migrations have been reported, there was a peak run-off period during the spring melt. Lake dwelling populations could be stimulated by the turbulence caused from inflowing streams (permanent or temporary) in the



spring, and turbulence in the littoral region of the lake as the ice breaks up. It would be interesting to know if this behavior originated with a river or a lake population. Regardless, the occurrence of this migratory behavior must be of significance to the biology of the species.

### Summary

The nymphal migration of *L. cupida* began during the spring break-up in the Bigoray River. The start of the migration was associated with a great increase in turbulence, and migration ceased when the river water level and turbulence decreased. Nymphs were day active during the migration, with the nymphs moving upstream along the river edges. The results of drift sampling agreed well with the diel activity pattern, with both migratory activity and drift reaching a peak shortly after mid-day. Gut analysis of the drift animals indicated a positive relationship between daily migratory numbers and the amount of feeding. There was also differential feeding by nymphs of different sizes. Average daily rates of movement were found to be about 100 meters per day.

The nymphs moved out of the river as they encountered the outlets of tributary areas. Nymphs in Tributary 1 moved as far as 1200 meters from the river, and a separation of size classes was accounted for by larger nymphs being able to move faster.

A parallel increase was found between degree days and periphytic diatom standing crop in the river and upper swamp of Tributary 1. Shortly after the beginning of the spring run-off, both standing crop of periphyton and degree days were greater in the swamp, but within two weeks, the river was accumulating more heat and had a greater standing crop of periphyton.



## POSTMIGRATION

### Postmigration Drift

After the migratory period, the *L. cupida* nymphs of the river exhibited the characteristic behavioral drift pattern of mayflies. Maximum numbers of nymphs were found in the drift during the 2200 to 2400 hour period (Figure 23). The specific shapes of the drift curves for each net are again somewhat different and, as was true of drift during the migration, this is felt to be due to river configuration and different filtering areas of the individual nets. The mayflies *Baetis tricaudatus* Dodds and *Callibaetis coloradensis* Banks also exhibited behavioral drift with maximum densities during the 2200 to 2400 hour period.

### Emergence

Using 12 emergence traps, located as shown in Figure 24, emergence was monitored daily for 16 days in 1969.

The first subimagos were trapped on 20 May at the north edge of the upper swamp (trap VI, Figure 25). The water temperature of the top 10 cm of water at this location was 12.0 C at this time. Subimagos came off this area in large numbers for 4 consecutive days, and then emergence around this trap tapered off. The day to day spatial pattern of emergence in the upper swamp over the first 2 weeks was related to the warming pattern of the water, the water becoming warmer first in the northern part of the swamp and then warming in a southerly direction. *L. cupida* began emerging from the southern part of the tributary area (trap II) on 22 May, and the first subimagos from the river were trapped on 28 May.

Emergence continued from the upper swamp throughout July. In the







Figure 23. *L. cupida* stream drift as monitored in the lower riffle (RA) following the migration of I970. See text for explanation of curves.

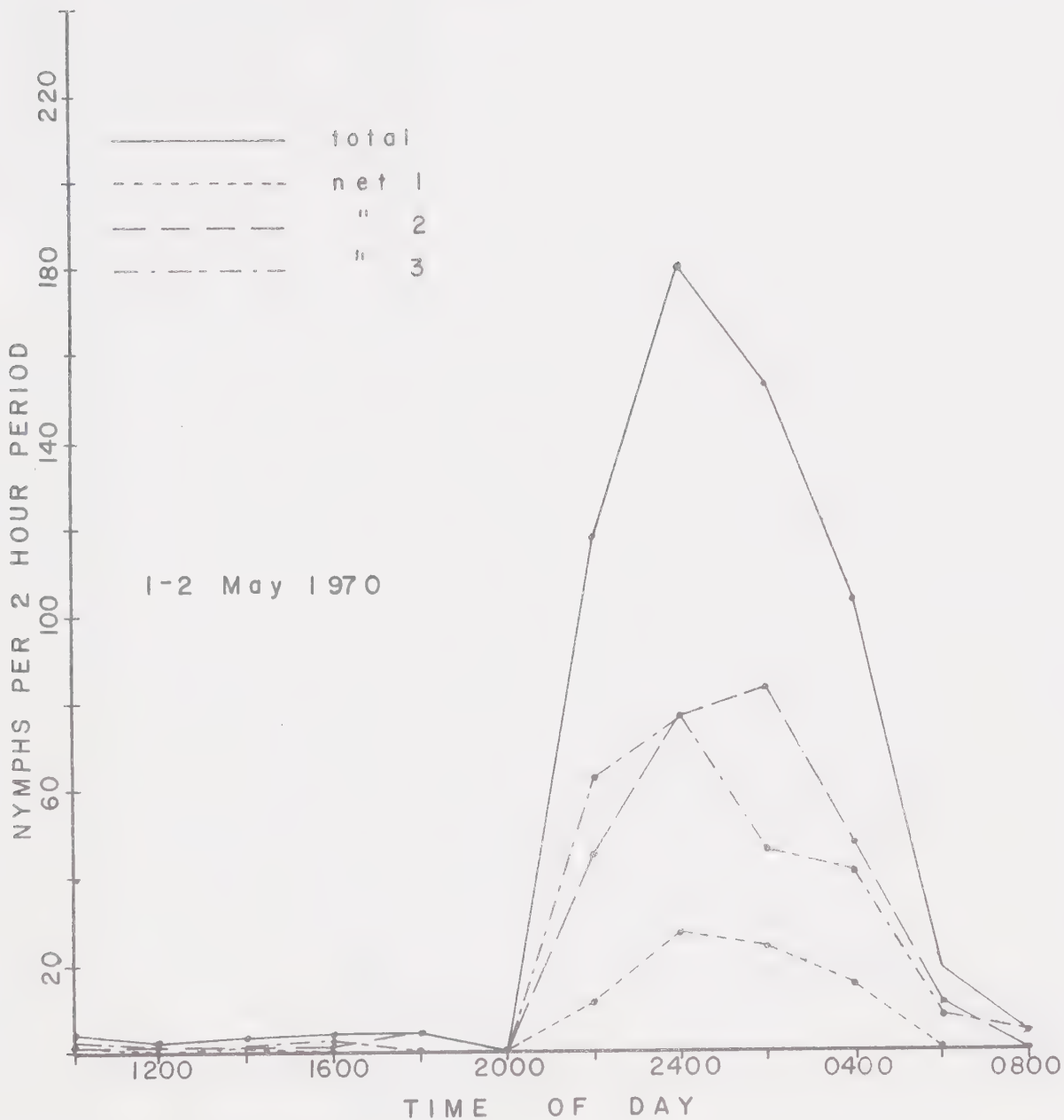






Figure 24. *Sites of emergence traps used in the study area,  
1969.*

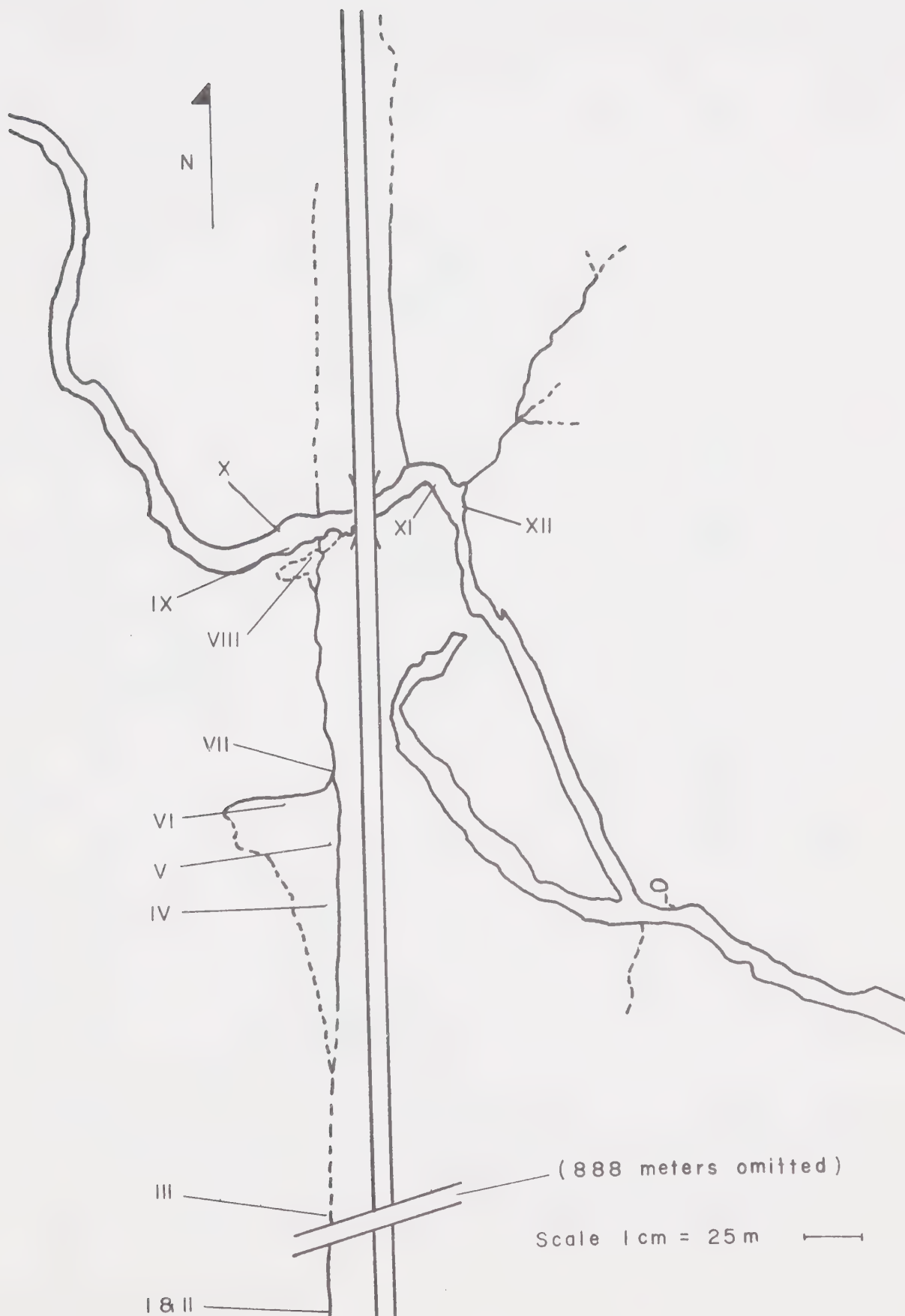
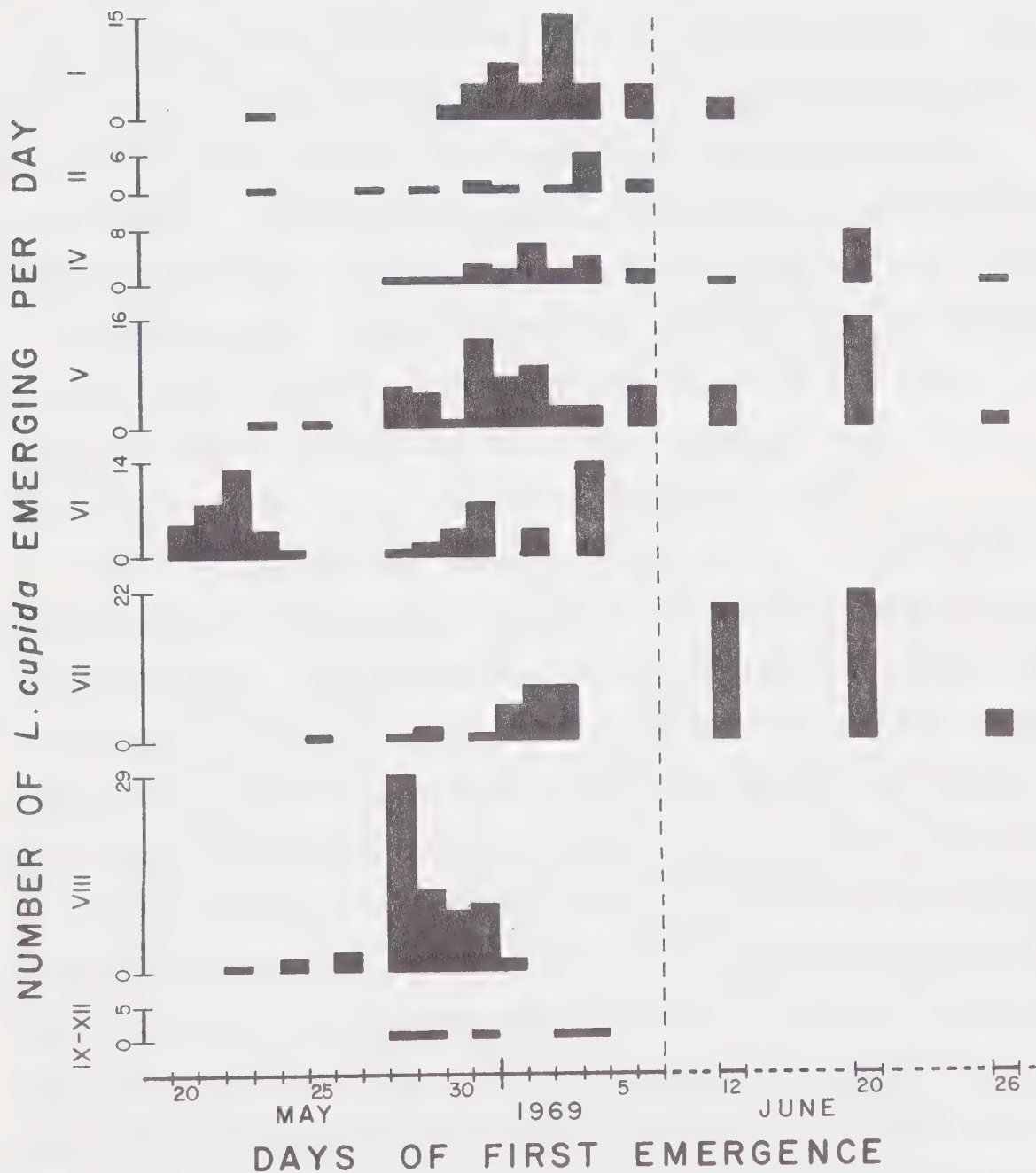








Figure 25.     *Numbers of L. cupida subimago collected in emergence traps, 20 May to 26 June 1969. Each mm on the vertical scale for each graph represents one subimago. Roman numerals on the ordinates indicate the trap sites.*





river some nymphs were collected on 20 September and placed in a laboratory aquarium at room temperature. These nymphs emerged the next day. Thus it appears possible that nymphs of the same generation were still transforming to subimagos in late September.

The average length of subimagos during the early days of emergence (20 May through 6 June 1969) was 12.0 mm, with individual lengths ranging from 10.5 mm to 14.0 mm. There was no decrease in average length during this period. After mid-June, there was a slight and gradual decrease in average lengths. As was true of male and female nymphs of a comparable age, female subimagos had an average length about 1 mm longer than male subimagos.

Emergence was most intense between 1200 and 1400 hours, but some emergence was observed as early as 0930 hours and as late as 1600 hours. This pattern did not conform with the daily water temperature cycle. Water temperatures usually reached a maximum at about 1800 hours.

Nymphs emerging from the tributary swam to the water's surface and grasped vegetation, permitting the dorsum of the thorax to break the surface film (Figure 26). The entire nymphal body was straightened and the cuticle split along the mesonotal suture. First the head was withdrawn from the nymphal exoskeleton and then the wings were slowly pulled from the wing pad casings. Transformation was completed when the wings were completely extended and the cerci were withdrawn from the nymphal skin. The entire process of transformation took less than 5 minutes. The subimagos then climbed up plant stems and were airborne within 2 or 3 minutes. Subimagos would launch onto their first flight during calm periods—wind or even a slight breeze would postpone this. Once they were in the air the mayflies appeared to have very little control over the direction of flight; they were carried with the wind, occasionally being lifted 15 to 30 meters off





- Figure 26.
- a. *A female L. cupida nymph transforming to the subimago. The wings of the subimago are half withdrawn from the nymphal skin, which can be seen just under the water surface.*
  - b. *Subimago immediately after emerging from the upper swamp of Tributary I.*







the ground. During the first 3 days of emergence, the subimagos from the upper swamp were dispersed both toward and away from the river, in practically all directions of the compass. As they first rose from the swamp flycatchers preyed heavily on them, and several times spiders (including *Xysticus* sp.) were seen carrying off newly emerged subimagos.

Unsuccessful attempts were made to follow and find the subimagos after they left their emergence sites. Traver (1925) found the subimagal stage to last for slightly less than 24 hours, but my own observations in the laboratory showed this stage to be shorter. Lyman (1944) points out the effect of ambient temperature on the final molt, and mentions that relative humidity also has a likely influence; hence my laboratory observations were not comparable to field conditions.

### Ovipositing

On 23 May 1969, 3 days after the first emergence, the female imagos were observed ovipositing in the Bigoray River. After the first emergence at least 20 man-hours were spent, at all hours of the day and at times a considerable distance from the study area, searching for mating swarms of imagos. None was seen and in fact the only imagos ever found in the field were actively ovipositing females or spent females taken from the surface drift. These first ovipositing imagos could have emerged as early as 20 May, since imagos emerging from a lab aquarium survived for as long as 5 days when they were kept in a humid environment.

Spieth (1940) reports members of the genus *Leptophlebia* to swarm over open areas some distance from open water. He also states that the timing of the nuptial dance and mating depend very much on environmental conditions. This was the case for ovipositing females in the Bigoray River. On 1 and



2 June 1969, surface drift nets collected spent and half spent females only during and shortly after hours when the sun was shining and the wind was relatively calm. No regular daily pattern of ovipositing, such as that seen for emergence, was apparent.

Female imagos did not release all of their eggs at one time, but dipped down repeatedly to the water's surface to deposit eggs. If the sun for a time became obscured while the female was actively ovipositing, the female imago would quickly fly to vegetation along the river bank and resume ovipositing only when the sun reappeared.

In the river, ovipositing was observed mainly in the two pools, but several times females were seen dipping down to the water in both riffle regions. These female imagos always flew in mid-channel and were oriented upstream. Ovipositing was never observed in the upper swamp, and during the summer and autumn only one nymph of the new generation was ever found in the upper swamp. However, a large number of *C. coloradensis* nymphs of the new generation were collected in the upper swamp during the summer.

The earliest *L. cupida* nymphs of the new generation were taken from the river on 20 June, and they were consistently collected with the pump sampler from then on. It appears that the earliest instars inhabit a different habitat in the stream than do the larger nymphs, because very small nymphs were never collected from the grassy undercut bank areas, which yielded many large nymphs.

### Discussion

Data indicate that emergence continued from late May to possibly as late as September, a period of 4 months. This is a much more extensive emergence period than that reported by Peters and Warren (1966) for



*L. cupida* in northwestern Arkansas (mid-March through April). And it is considerably longer than Clifford (1969) believed for this species in the Bigoray River. The large number of habitats, each with a different thermal regime, probably accounted for the long emergence period in the Bigoray River area. Spatial separation of the old generation nymphs of different developmental ages into areas of different temperature conditions, and caused initially by the migration, would further prolong the emergence.

It is not known whether the subimagos emerging late in the season were successful in mating or even if their eggs were viable. Therefore, delayed hatching of eggs, as Clifford (1969) has postulated, may be the cause of the wide range of nymphal sizes found in the *L. cupida* population, but I favor the idea of a prolonged period of emergence and oviposition to explain the size and age structure of the nymphal population.

#### Summary

Following the migration, *L. cupida* nymphs showed a behavioral drift pattern with maximum numbers drifting during the night, which was an approximate 12 hour shift from their diel drift pattern during the migration.

Emergence began in late May and may have continued into September. This could then be the cause of the wide range in nymphal sizes of this species in the Bigoray River population. Alternatively, delayed hatching of eggs may have affected the nymphal size composition.

Almost all of the female imagos oviposited in the river instead of in the upper swamp, from which many emerged. Emergence was most intense at about mid-day, but no daily pattern was found for the ovipositing phenomenon. Instead, weather conditions influenced the daily periods of egg laying.





## GENERAL DISCUSSION

### Adaptive Significance of the *L. cupida* Migration

The significance of the *L. cupida* nymphal migration cannot be entirely understood from the results of a study in one rather restricted area. Factors that would seem to be advantageous in one location may have no apparent significance in another location. The adaptive advantage of migratory behavior must then be considered in regard to how it affects the entire migratory population of the species.

Neave (1930) suggested there is survival value for *L. cupida* nymphs migrating away from the scouring action of river or lake ice, occurring during the break-up. Since the preferred habitats of the nymphs is near the bank and shore line areas, this reasoning is sound, especially for the evolution of the migratory behavior in lake populations.

Range extension by migration into tributary areas might be considered an advantage, especially in terms of population survival, but post-emergence dispersal of the subimagos seemed to be of even greater significance in this respect. Furthermore, the extension of range in my study was restricted to nymphs of the migrating generation; nearly all of the ovipositing occurred back in the river.

Avoidance of fish predation would be of survival advantage to the migratory nymphs. But this did not appear to be an important factor in the Bigoray River, where the fish community was restricted mainly to spawning suckers (*Catostomus commersonii* (Lacepède) and *C. catostomus* (Forester)) that came up from the Pembina River in late May or early June, returning to the Pembina River within about a month (W.A. Bond, personal communication). In other geographical areas, fish predation could be of





much greater significance, and movement from fish inhabited areas would be most advantageous to *L. cupida* nymphs.

Bird predation, especially by waterfowl, may have been less likely in the tributary areas than in the river. Ducks were often seen on the river in the spring, but much less frequently in the tributary areas.

Dytiscid larvae were seen in Tributary 1 as early as 9 April 1969, and later these larvae were observed preying on *L. cupida* nymphs. Furthermore, it appeared that predaceous insects were more abundant in Tributary 1 than in the river, but tributary migration areas described by Traver (1925), Neave (1930), and Ide (1935) seem to have had fewer predatory aquatic insects.

My data for Tributary 1 did not support the hypothesis that temperature and food conditions for the nymphs would be improved by the nymphs moving into tributary areas. But my study area may be different from other migratory areas. Temperatures of the upper swamp were lowered by the inflow of cold water from bordering muskeg areas, but the daily variation was much greater in the upper swamp than in the river. It is possible that these temperature fluctuations may have had stimulating effects on nymphal maturation and their eventual metamorphosis. Perhaps it was advantageous for nymphs to be initially in warmer water after their migration.

Swampy areas away from the river certainly provided an abundance of emergence sites, but it seems doubtful that a lack of emergence sites would in any way limit emergence from the river.

Definite negative aspects of migratory behavior would be the tremendous energy expenditure required in moving great distances upstream, and the possibility of mortality caused by the nymphs becoming trapped in the ice and freezing during cold nights.



A number of birds are predaceous on adult mayflies, and some birds may prey on the nymphs as well. It would seem that a concentration of nymphs in a shallow tributary area would be a more productive hunting ground for insectivorous birds. Several times during the migration, birds (possibly the eastern phoebe, *Sayornis phoebe* (Latham), appeared to be feeding on *L. cupida* nymphs as the nymphs were migrating along the river's edge. Later, greater yellowlegs, *Totanus melanoleucus* (Gmelin), which are known to feed on aquatic insect larvae, were common in the upper swamp. But, as mentioned previously, waterfowl were more commonly seen on the river.

More important would be the possibility of the swampy areas drying up before emergence could be accomplished. The emigrant nymphs did seem to select deeper water areas of the tributary swamps as postmigration habitats, and no evidence of mortality due to their habitat drying up was ever found.

This is by no means a complete summary of possible beneficial and detrimental aspects of the *L. cupida* migration. The positive consequences must outweigh or have outweighed negative consequences of migration, since natural selection is or has been the ultimate factor involved in the evolution of this behavior pattern.

The major advantage of this migration in the Bigoray River is that it allows the nymphs to undergo final nymphal maturation in areas isolated from the disruption of late spring and early summer flooding. In lake populations, the avoidance of the scouring effect of edge ice is perhaps the most important advantage for the migratory nymphs.

#### *L. cupida* Migration in Relation to General Insect Migration

Workers have recently been able to enumerate some characteristics of



general migratory behavior (Kennedy 1961, Southwood 1962, Carthy 1965, Johnson 1969), mainly from the study of adult insects. Most of what is known about endocrine control of locomotor activity has been gained from research with insect nymphs, and it yet remains for these latter findings to be compared and found similar to hormonal action in adult insect migrants. With this in mind I thought it might be useful and interesting to compare several general characteristics of adult insect migration with the nymphal migration of *L. cupida*.

(1) *Migratory movement usually occurs early in the life of an adult insect.* If this were strictly the case with *L. cupida*, the migration would be extremely short-lived; but if one interprets this to mean some sort of developmental stage prior to sexual maturation, it would fit in well with *L. cupida* nymphs. Although nymphs of various sizes were observed migrating, physiological development of all these nymphs may have been at nearly the same stage. Clifford (1970) has shown that total length measurements are a poor indication of the degree of maturation for *L. cupida* nymphs.

(2) *During migratory movement insects often show a positive response to light.* The daily duration of movement (Figure 17) and the drift rates (Figure 18) indicate that *L. cupida* does have a positive response to light during the migration. This is apparently a daily shift of about 12 hours in their activity pattern when compared to their activity during non-migratory periods of the year. Water turbulence and velocity initiate the overall behavior of migration by the nymphs, but it is a subsequent reaction to light which controls the daily duration of their migratory movement.

(3) *There is a suspension of growth-promoting activities during migration.* These activities encompass much more than feeding, since obviously starved animals could not migrate for long (Hocking 1953).





*L. cupida* nymphs do feed during migration, but it is unlikely that much or any of the energy obtained is directed towards growth during this period. What is important here is that foraging is secondary to migratory activity.

(4) *Migrations are characterized by having a fixed daily period during which there is persistent locomotor activity.* The daily activity curve of the *L. cupida* nymphs supports this, but individual nymphs were not constantly observed. If the above hypothesis does in fact hold true for *L. cupida*, it would lend support to my observation that individuals actively migrated for only 10 hours per day, but it does not exclude the possibility that some nymphs may migrate for the entire daylight period.

(5) *There is a higher level of migratory behavior in insects from temporary habitats than from permanent habitats.* This hypothesis is mainly concerned with comparisons of different taxa; but, in view of a possible polymorphic population (Kennedy 1961), it also seems applicable to different populations within a taxon. During ice break-up the winter habitat of *L. cupida* in all known geographical regions where migration has been reported would be unstable and thus temporarily unsuitable for the duration of high water run-off. *L. cupida* populations that live in geographical areas where great seasonal fluctuations in water level or turbulence do not occur might be expected not to migrate, and as far as is known this is the case.

(6) *Migratory movements frequently result in an increase in the mean distance between individuals.* This was not the case for the *L. cupida* population that migrated into the upper swamp of Tributary 1, but the density of nymphs in the river clearly did decrease.

The migration of *L. cupida* nymphs has many of the same general characteristics shown by other migratory insects, and it is likely that *L. cupida* undergoes many of the same physiological changes as the migratory





insects of other taxa. *L. cupida* is restricted to North America and its migratory behavior is suspected of being facultative (not occurring in certain areas) for the continental population of the species. It would be valuable to substantiate this by studies in areas with less severe seasonal water level fluctuations.



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## APPENDIX

### Comparative Sampling

In an effort to measure the reliability of the pump method and to compare it with the Surber sampler and Ekman dredge, a series of 40 samples were taken from the two pools (PA & PB) and two riffles (RA & RB) of the Bigoray River between 27 May and 31 May 1969. Starting in RA, 5 pairs of samples were taken with the Surber and the pump samplers; the procedure being to collect first the Surber sample and then, with the Surber frame still in the stream, to place the pipe of the pump directly beside the frame. The sample pairs were taken in an upstream sequence; hence the stream bottom was not disturbed prior to sampling. The same procedure was used in the pools except that an Ekman dredge, rather than the Surber sampler, was paired with the pump. By taking the samples in this manner any bias caused by taking sample pairs close together would be in favor of the "standard" method. The actual sampling area of each sampler was: 930 cm<sup>2</sup> for the Surber, 320 cm<sup>2</sup> for the pump, and 240 cm<sup>2</sup> for the Ekman dredge. Hence the total area sampled by the Surber was approximately three times the area sampled by the pump or Ekman dredge.

Each riffle and each pool was sampled in a single day and the animals were removed from all 10 samples from each habitat on the day of sampling or the next day. Before the invertebrates were picked out, all samples were washed in a bucket with a screen bottom (0.5 mm mesh opening size). The results are presented in Tables A1 through A4.

One of the most noticeable features of the tabulated data is the



high values of the standard error. This indicates that these means are unreliable as estimates of the actual average number of these animal groups in the river. This feature of stream invertebrate sampling has previously been shown by Needham and Usinger (1956), and appears to be due mainly to the great variety of habitats in streams. Still, a comparative examination of the paired samples is important for indicating the efficiency and character of each method.

In RA (Table A1), the pump appears to sample all taxa except Simuliidae more efficiently than did the Surber sampler, but in RB (Table A2) more taxa were collected with the Surber sampler. The main difference between the two riffles was the composition of the substrate, which in RA was of small gravel and sand or clay, and of large rocks in RB. Because of this, the pipe for the pump sampler was more easily placed in RA, and much more substrate material was pumped up. Interstitial spaces deep in the substrate are known to be a habitat for many "non-burrowing" aquatic insects (Coleman and Hynes, 1969), and it appears that if this zone is composed of gravel the pump sampler is more effective. The coarse, rocky bottom makes placement of the pump pipe difficult, and less bottom material is taken up with the sample; hence more insects are able to maintain position under the larger rocks and are not taken up by the sucking action of the pump. When using the Surber sampler, these stones are usually turned over and scrubbed, but apparently most of this zone was left undisturbed by the pump. It is also interesting that horsehair worms (*Gordius* sp.) were collected from the riffles only with the Surber sampler.

The pump and Ekman samples were quite similar (Tables A3 and A4). Large benthic animals, especially the burrowing forms, were collected more readily with the pump, but some of the smaller animals, such as Chironomidae,



Table A1. *Results of sampling with the Surber sampler and the pump sampler in riffle RA during the postmigration period, 27 May 1969.*

Taxa	Surber sampler		Pump sampler	
	Number per m <sup>2</sup>	Standard error	Number per m <sup>2</sup>	Standard error
<i>Baetis tricaudatus</i>	170	44	382	174
<i>Hydropsyche slossonae</i>	80	30	369	168
<i>Cheumatopsyche analis</i>	43	24	134	66
<i>Agraylea</i> sp.				
Limnephilidae				
Coleoptera adults	71	38	197	108
Coleoptera larvae	17	12	115	51
Simuliidae	1191	855	1146	487
Chironomidae	77	20	439	199
<i>Hyallela azteca</i>				
other Insecta	15	10	70	40
other non-Insecta	7	4	13	8
Oligochaeta	present		common	

Note: Taxa with a density less than 25 animals/m<sup>2</sup> in either RA or RB are included in the "other" categories. Five samples were taken in each area with each method.



Table A2. Results of sampling with the Surber sampler and the pump sampler in riffle RB during the postmigration period, 30 May 1969.

Taxa	Surber sampler		Pump sampler	
	Number per m <sup>2</sup>	Standard error	Number per m <sup>2</sup>	Standard error
<i>Baetis tricaudatus</i>	514	123	369	171
<i>Hydropsyche slossonae</i>	94	61	32	18
<i>Cheumatopsyche analis</i>	260	129	51	13
<i>Agraylea</i> sp.	181	144	248	153
Limnephilidae	123	107	140	78
Coleoptera adults	125	41	159	44
Coleoptera larvae	30	17	45	24
Simuliidae	8708	7209	2369	1834
Chironomidae	909	465	777	424
<i>Hyallela azteca</i>	82	79	134	99
other Insecta	74	23	83	60
other non-Insecta	4	3	6	6
Oligochaeta	present		common	

Note: Taxa with a density less than 25 animals/m<sup>2</sup> in either RA or RB are included in the "other" categories. Five samples were taken in each area with each method.





Table A3. *Results of sampling with the Ekman sampler and the pump sampler in pool PA during the postmigration period, 28 May 1969.*

Taxa	Ekman sampler		Pump sampler	
	Number per m <sup>2</sup>	Standard error	Number per m <sup>2</sup>	Standard error
<i>Baetis tricaudatus</i>				
<i>Callibaetis coloradensis</i>			13	13
<i>Cloeon</i> sp.				
<i>Caenis simulans</i>	17	17	45	45
<i>Sialis cornuta</i>			45	45
<i>Cheumatopsyche analis</i>			25	25
Limnephilidae	25	25	45	28
<i>Agraylea</i> sp.	8	8	19	13
Coleoptera adults	21	12	32	18
Chironomidae	2608	900	2025	807
other Insecta	33	16	77	33
other non-Insecta	183	119	185	126
Oligochaeta	abundant		abundant	

Note: Taxa with a density less than 25 animals/m<sup>2</sup> in either PA or PB are included in the "other" categories. Five samples were taken in each area with each method.



Table A4. *Results in sampling with the Ekman sampler and the pump sampler in pool PB during the postmigration period, 31 May 1969.*

Taxa	Ekman sampler		Pump sampler	
	Number per m <sup>2</sup>	Standard error	Number per m <sup>2</sup>	Standard error
<i>Baetis tricaudatus</i>	383	333		
<i>Callibaetis coloradensis</i>	17	17	147	88
<i>Cloeon</i> sp.	50	24	32	14
<i>Caenis simulans</i>	59	21	13	8
<i>Sialis cornuta</i>	25	17	38	19
<i>Cheumatopsyche analis</i>			6	6
Limnephilidae	50	33	26	19
<i>Agraylea</i> sp.	108	89	32	24
Coleoptera adults	33	33	26	12
Chironimidae	3067	790	2509	855
other Insecta	42	32	64	25
other non-Insecta	17	10	64	25
Oligochaeta	abundant		abundant	

Note: Taxa with a density less than 25 animals/m<sup>2</sup> in either PA or PB are included in the "other" categories. Five samples were taken in each area with each method.



were probably lost through the mesh of the collecting bag on the pump discharge. One difference not shown by Tables A3 & A4 was that the few *Hexagenia limbata* (Serville) and *Doniccia* sp., which are grouped into the "other Insecta" category, were collected only with the pump. However, climbing nymphs of *Callibaetis coloradensis* were collected in greater numbers by the pump, as would be expected since with this method the entire water column is sampled. This is an important advantage, especially in streams, over the Ekman dredge.

To estimate numbers of biomass per square meter with any degree of accuracy a great many more samples would have to be collected, regardless of the sampling method. All three sampling methods are at best "semi-quantitative." Without knowing the actual composition of the aquatic community, it is difficult to judge which method would yield the most accurate estimate of the invertebrate fauna. In the riffles a total of 25 taxa were collected by the Surber sampler and 25 taxa were collected by the pump. In the pools, 20 taxa were collected by the Ekman dredge and 27 taxa were collected by the pump. Thus, in the pools, the pump collected a somewhat more diverse fauna than did the Ekman dredge.

As mentioned in the Methods section, the main advantage of the pump is that it could be used in both riffles and pools. Furthermore, the pump was equally effective in all seasons of the year. Invertebrates that adhere to the substrate (e.g., Simuliidae), especially when attached to rooted vegetation, are not efficiently sampled with the pump, whereas other groups of invertebrates are collected only by the pump.

In retrospect, several modifications of the pumping procedure would increase its efficiency. A stronger pipe fitted with handles would permit it to be more firmly placed into the stream bottom. Manual stirring of the



substrate within the pipe, especially if the substrate is coarse, should yield more of the total stream fauna. The use of a more portable model of pump (e.g., a two inch Edson pump) would allow the sampler to be more easily moved from area to area, and samples could also be taken from a boat.











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